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IDAHO COOPERATIVE FISH AND WILDLIFE RESEARCH UNIT

ADULT PACIFIC LAMPREY MIGRATION IN THE LOWER COLUMBIA RIVER: 2007 RADIOTELEMETRY AND HALF-DUPLEX PIT TAG STUDIES

A Report for Study Code ADS-P-00-8

by

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For

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Portland District, Portland OR

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14. ABSTRACT

Monitoring Pacific lamprey (Lampetra tridentata) run size and migration behaviors in the Columbia River basin is difficult given their cryptic and photo-negative behaviors. In this study we tagged lamprey with half duplex (HDX) passive integrated transponder (PIT) tags and radio transmitters and monitored their passage at Bonneville, The Dalles, John Day, McNary, and Ice Harbor dams. Our objectives were to calculate lamprey passage times, to estimate escapement past the monitored sites and to evaluate potential correlates with lamprey passage success. In 2007, we radio-tagged 398 lamprey and HDX-PIT tagged 757 lamprey. Conversion estimates from release below Bonneville Dam to top-of-ladder antennas were 21% for radio-tagged fish and 52% for HDX-PIT tagged fish. Conversions from the top of Bonneville Dam to top-of-ladder antennas at The Dalles Dam were 25% for radio-tagged fish and 63% for HDX-PIT tagged fish. Conversions from the top of The Dalles Dam to top-of-ladder antennas at John Day Dam were 43% for radiotagged fish and 52% for HDX-PIT tagged fish. Large lamprey in both the telemetry and HDX-PIT studies were significantly more likely than small lamprey to pass through most of the monitored damto- dam reaches. Lamprey migration times were highly variable, but tended to be slow at dams and relatively rapid through reservoirs. Median passage times for radio-tagged fish were 7.6 days from release past Bonneville Dam, 3.8 days between top-of-ladder antennas at Bonneville and The Dalles dams, and 2.4 days between antennas at The Dalles and John Day dams. Median times for HDX-PIT tagged lamprey over these same reaches were 6.5 days, 4.0 days, and 4.3 days, respectively. Lamprey with both tag types migrated more rapidly later in the season, coincident with increasing river temperatures and decreasing river discharge. Higher conversion rate estimates by HDX-PIT tagged fish, compared to radio-tagged fish, may have been related to negative radio-tag effects or transmitter failure but our analyses of these effects were somewhat inconclusive. In future studies, double-tagging with both PIT and radio tags should help resolve questions regarding tag effects and detection efficiencies across monitoring types and sites.

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Abstract

Monitoring Pacific lamprey (*Lampetra tridentata*) run size and migration behaviors in the Columbia River basin is difficult given their cryptic and photo-negative behaviors. In this study we tagged lamprey with half duplex (HDX) passive integrated transponder (PIT) tags and radio transmitters and monitored their passage at Bonneville, The Dalles, John Day, McNary, and Ice Harbor dams. Our objectives were to calculate lamprey passage times, to estimate escapement past the monitored sites, and to evaluate potential correlates with lamprey passage success.

In 2007, we radio-tagged 398 lamprey and HDX-PIT tagged 757 lamprey. Conversion estimates from release below Bonneville Dam to top-of-ladder antennas were 21% for radio-tagged fish and 52% for HDX-PIT tagged fish. Conversions from the top of Bonneville Dam to top-of-ladder antennas at The Dalles Dam were 25% for radio-tagged fish and 63% for HDX-PIT tagged fish. Conversions from the top of The Dalles Dam to top-of-ladder antennas at John Day Dam were 43% for radio-tagged fish and 52% for HDX-PIT tagged fish. Large lamprey in both the telemetry and HDX-PIT studies were significantly more likely than small lamprey to pass through most of the monitored dam-to-dam reaches.

Lamprey migration times were highly variable, but tended to be slow at dams and relatively rapid through reservoirs. Median passage times for radio-tagged fish were 7.6 days from release past Bonneville Dam, 3.8 days between top-of-ladder antennas at Bonneville and The Dalles dams, and 2.4 days between antennas at The Dalles and John Day dams. Median times for HDX-PIT tagged lamprey over these same reaches were 6.5 days, 4.0 days, and 4.3 days, respectively. Lamprey with both tag types migrated more rapidly later in the season, coincident with increasing river temperatures and decreasing river discharge.

Higher conversion rate estimates by HDX-PIT tagged fish, compared to radio-tagged fish, may have been related to negative radio-tag effects or transmitter failure but our analyses of these effects were somewhat inconclusive. In future studies, double-tagging with both PIT and radio tags should help resolve questions regarding tag effects and detection efficiencies across monitoring types and sites.

Introduction

Pacific lamprey (*Lampetra tridentata*) is the largest lamprey species in the Columbia and Snake rivers. Pacific lampreys are anadromous, with parasitic adults spending 1-4 years in the ocean before returning to spawn in freshwater rivers (Beamish 1980; Close et al. 2002; Moser and Close 2003). Recent studies suggest that Pacific lamprey abundance has steadily declined in the Columbia River basin and in other regional rivers since the early 1960's (Close et al. 2002; Kostow 2002). Habitat loss, river impoundment, ocean conditions, and water pollution have all likely contributed to the decline. Lampreys are also relatively poor swimmers and have difficulty passing through Columbia and Snake River dam fishways designed for adult salmonids (Moser et al. 2002b; Johnson et al. *in review*).

Monitoring Columbia River basin lamprey populations has been a challenge. Lamprey counts at dam fish ladders can only be used as indicators of relative abundance and general run timing because counts generally take place only during the day and most lamprey passage occurs at night (Moser et al. 2002a; Robinson and Bayer 2005). Radiotelemetry has been used in a series of studies over the last decade in an effort to improve monitoring, identify problem passage areas, and estimate survival of adult Pacific lamprey in the basin (e.g., Moser et al. 2002b; 2005). Starting in 2005, half duplex (HDX) passive integrated transponder (PIT) tag monitoring sites have also been deployed at dams to monitor larger samples of PIT-tagged adult lamprey. Like radio transmitters, PIT tags are uniquely identifiable, allowing monitoring of individual fish. PIT tags are also relatively small and inexpensive and are not limited by battery life, a useful feature given that some adult lamprey overwinter in the Hydrosystem (Daigle et al. 2008). HDX-PIT tags were selected for Pacific lamprey passage evaluations to avoid potential tag collisions with the full-duplex (FDX) PIT tags used to monitor salmonids in the basin.

The objectives of the 2007 studies described in this report were to use both radiotelemetry and HDX-PIT systems to: 1) calculate adult lamprey passage rates past multiple dams and reservoirs; 2) estimate lamprey conversion (i.e., escapement) past multiple dams and through individual dam-to-dam reaches; 3) examine potential physiological and environmental correlates with passage success; and 4) compare results by tag type. Results from an additional study objective, describing fine-scale lamprey passage behaviors at individual dams, will be presented in separate reports.

Methods

Fish Collection and Tagging

Lampreys used in this study were collected at night in traps at Bonneville Dam (Columbia River kilometer [rkm] 235). Traps were located near the Adult Fish Facility and at the Washington-shore fishway entrance. In 2007, 757 lamprey were tagged with half-duplex passive integrated transponder tags (HDX-PIT), and 398 were tagged with radio transmitters. No fish with girth < 9 cm at the dorsal fin were radio-tagged. All HDX-PIT fish were released approximately three kilometers downstream near Hamilton Island. Radio-tagged fish were released near Hamilton Island (*n* = 207) or near Tanner Creek (*n* = 191) at Columbia River rkm 232.5.

Before tagging, all fish were anaesthetized using 60 ppm (3 mL•50 L^{-1}) clove oil, and measured (length and girth to the nearest mm), and weighed (nearest g). HDX-PIT fish were then outfitted with a uniquely-coded glass encapsulated HDX-PIT tag (Texas Instruments, 4×23 mm, 0.8 g). HDX-PIT tags were surgically implanted in the body cavity of anaesthetized fish through a small incision (< 1 cm) along the ventral midline and in line with the anterior insertion of the first dorsal fin as described in Moser et al. (2006). Uniquely-coded radio tags (30.1 mm length, 9.1 mm diameter, 4.5 g in water;

model NTC-6-2, Lotek Wireless Inc.) were surgically implanted using the methods described in Moser et al. (2002a). An additional physiological measure, muscle lipid content (% fat), was collected for radio-tagged fish using a Distell fat meter (e.g., Crossin and Hinch 2005).

Monitoring Sites

Lamprey movements were monitored using an array of fixed-site radiotelemetry antennas and receivers (Table 1) and HDX-PIT interrogation sites (Table 2). Radio receivers at the lower Columbia River dams were equipped with digital spectrum processors to receive transmissions on several frequencies simultaneously. Aerial antennas were used to monitor dam tailraces and several tributary confluence areas (Deschutes, Umatilla, Walla Walla, and Yakima rivers). Underwater antennas detected radio-tagged fish as they approached, entered, and exited fishway openings as well as movements inside fishways and transition pools and exits from ladders into dam forebays. (Note: dam maps showing all monitoring sites are included in Appendix A.)

Underwater HDX-PIT antennas were located inside dam fishways at the four lower Columbia River dams and at Ice Harbor Dam. Antennas were located near top-of-ladder exits at all dams. At Bonneville Dam, additional sites were located at lamprey bypass structures, inside the Washington-shore entrance, and in the Cascades Island fishway. Antennas were also located near transition pools and/or the overflow weir portions of ladders at McNary and Ice Harbor dams (Table 2).

Data Analyses

Reach conversion rates were calculated by dividing the number of lamprey known to pass an upstream HDX or telemetry site by those known to pass a downstream site or by the number released. Fish were treated as passing a site if they were detected at the site or were detected at a location further upstream. Conversion rates were calculated within year across all release dates as well as for individual release days and blocks of days to evaluate seasonal effects. Lamprey sizes — including length, weight, and girth — were compared for groups that successfully migrated through a reach and those of unsuccessful fish using general linear models (PROC GLM, SAS) and analysis of variance.

Lamprey migration times (d) and passage rates ($km \bullet d^{-1}$) were calculated from release to top-of-ladder HDX-PIT and telemetry antennas at dams and between monitored sites. Linear regression was used to evaluate relationships between log-transformed lamprey passage times and fish size (length, girth, weight), release date or date fish entered upstream reaches, and river discharge and water temperature either on the release date or the date each fish passed top-of-ladder sites at dams. Analyses using environmental data should be considered qualitative as it was difficult to assign representative metrics given the variable and often long passage times.

Detection efficiencies for both HDX-PIT and radiotelemetry sites were estimated by dividing the number of fish known to pass a site by the number detected. These estimates were imprecise because fish could pass via alternate routes at many locations (e.g., navigation locks). It was unknown how many fish passed undetected at any dam, and estimated efficiencies provide a largely qualitative description.

Table 1. Telemetry receiver and antenna sites used to monitor lamprey passage at lower Columbia River dams in 2007. (Note: additional telemetry sites were used at Priest Rapids Dam and at Snake River dams upstream from Ice Harbor Dam.)

		Antenna(s)	
Site	Location	Type	Number
Bonneville Dam	Tailrace	Aerial	2
	PH 1, South-shore entrance	Underwater	3
	PH 1, North-shore entrance	Underwater	5
	PH 1, A-Branch transition pool	Underwater	3
	PH 1, A- and B-Branch junction pool	Underwater	4
	PH 1, Bradford Island lamprey channel	Underwater	3
	PH 1, Bradford Island exit	Underwater	1
	B-Branch entrance	Underwater	4
	B-Branch transition pool	Underwater	3
	Cascades Island entrance	Underwater	4
	Cascades Island transition pool	Underwater	4
	Cascades Island makeup water channel	Underwater	9
	PH 2, South-shore entrances	Underwater	7
	PH 2, North-shore entrances	Underwater	7
	PH 2, WA-shore transition pool	Underwater	6
	PH 2, WA-shore ladder and turnpool	Underwater	4
	PH 2, WA-shore entrance lamprey trap	Underwater	3
	PH 2, WA-shore ladder / UMT channel pool	Underwater	3
	PH 2, WA-shore ladder lamprey channel	Underwater	3
	PH 2, WA-shore counting window	Underwater	5
	PH 2, WA-shore ladder exit	Underwater	1
The Dalles Dam	Tailrace	Aerial	5
	South spillway entrance	Underwater	2
	Powerhouse entrances	Underwater	4
	East ladder entrance	Underwater	5
	East ladder transition pool	Underwater	5
	East ladder exit	Underwater	1
	North ladder entrance	Underwater	1
	North ladder entrance / transition pool	Underwater	5
	North ladder exit	Underwater	1
John Day Dam	Tailrace	Aerial	2
	South ladder exit	Underwater	1
	North ladder exit	Underwater	1
McNary Dam	Tailrace	Aerial	2
	South-shore entrance	Underwater	4
	South-shore transition pool / ladder	Underwater	7
	South ladder exit	Underwater	3
	North powerhouse entrance	Underwater	5
	North-shore entrance	Underwater	3
	North-shore transition pool / ladder	Underwater	5
	North ladder exit	Underwater	3

Table 2. Half-duplex PIT tag interrogation sites (antennas) used to monitor lamprey passage at lower Columbia and Snake river dams n 2007. NOAA-Fisheries maintained sites in the Bonneville lamprey bypass systems and at the Cascades Island fishway site. See Daigle et al. (2008) for maps showing antenna sites.

Site	Location	Number of antenna(s)
Bonneville Dam	PH 1, Bradford Island lamprey bypass	4
	PH 1, Bradford Island exit	1
	PH 2, WA-shore entrance	3
	PH 2, WA-shore ladder	4
	PH 2, WA-shore exit	1
	PH 2, WA-shore lamprey bypass	2
	Cascades Island	1
The Dalles Dam	Below East ladder count window	4
	East ladder exit (above count window)	4
	North ladder exit	3
John Day Dam	South ladder exit	1
	North ladder exit	1
McNary Dam	South-shore transition pool / ladder	4
	South-shore exit	3
	South-shore juvenile channel near exit	2
	North-shore transition pool / ladder	4
	North-shore exit	1
Ice Harbor Dam	South-shore entrance	2
	South-shore transition pool / ladder	4
	South-shore exit	1
	North-shore transition pool / ladder	4
	North-shore exit	4

Results

Lamprey Tagging

Size metrics for the lamprey radio-tagged in 2007 were all positively correlated (length×girth r^2 = 0.78; length×weight r^2 = 0.88; length×%fat r^2 = 0.13; girth×weight r^2 = 0.94; girth×%fat r^2 = 0.18; weight×%fat r^2 = 0.18) (Figure 1). Percent fat was more variable (coefficient of variation [CV] = 30.4%) than weight (20.3%), girth (8.2%), or length (7.6%) (Table 3). None of the size metrics was correlated with fish release date ($r^2 \leq 0.03$).

On average, HDX-PIT tagged lampreys were smaller than radio-tagged fish (Table 3) at least in part because of the 9 cm girth restriction for radio tagging. However, correlations among size metrics for HDX-PIT tagged fish were similar to those for radio-tagged fish: length×girth r^2 = 0.63; length×weight r^2 = 0.81; girth×weight r^2 = 0.90 (Figure 2). As with radio-tagged fish, weight was more variable (CV = 21.7%) than either girth (8.3%) or length (7.7%); % fat data were not collected. Lamprey HDX-PIT tagged early in the migration were larger than those tagged later in the migration (linear regression, $P < 0.05$); however, date explained a very small portion of the variability in the size data ($r^2 \leq 0.04$).

Tagging effort differed for the two tag types (Figures 3 and 4). Radio-tagging occurred from 1 June through 8 August, with the effort concentrated during traditional peak passage months of June and July. The relatively late migration timing for the run in 2007 resulted in proportionately higher radio-tagging rates early compared to late in the run (Figure 3). HDX-PIT tagging occurred from 24 May through 20 August, with blocks of effort in early, mid- and late season (Figure 4).

Table 3. Length, girth, and weight of lampreys collected and tagged with HDX-PIT or radio tags at Bonneville Dam in 2007. (Total *n* = 398 radio and 757 HDX-PIT.)

	Length (cm)			Girth (cm)			Weight (g)			Percent fat (%)		
Type	*n*	Mean	*sd*	*n*	Mean	*sd*	*n*	Mean	*sd*	*n*	Mean	*sd*
Radio	397	65.8	5.0	398	11.0	0.9	398	465.4	94.4	385	9.52%	2.89%
HDX-PIT	755	64.8	5.0	756	10.9	0.9	755	445.2	96.7	--	--	--

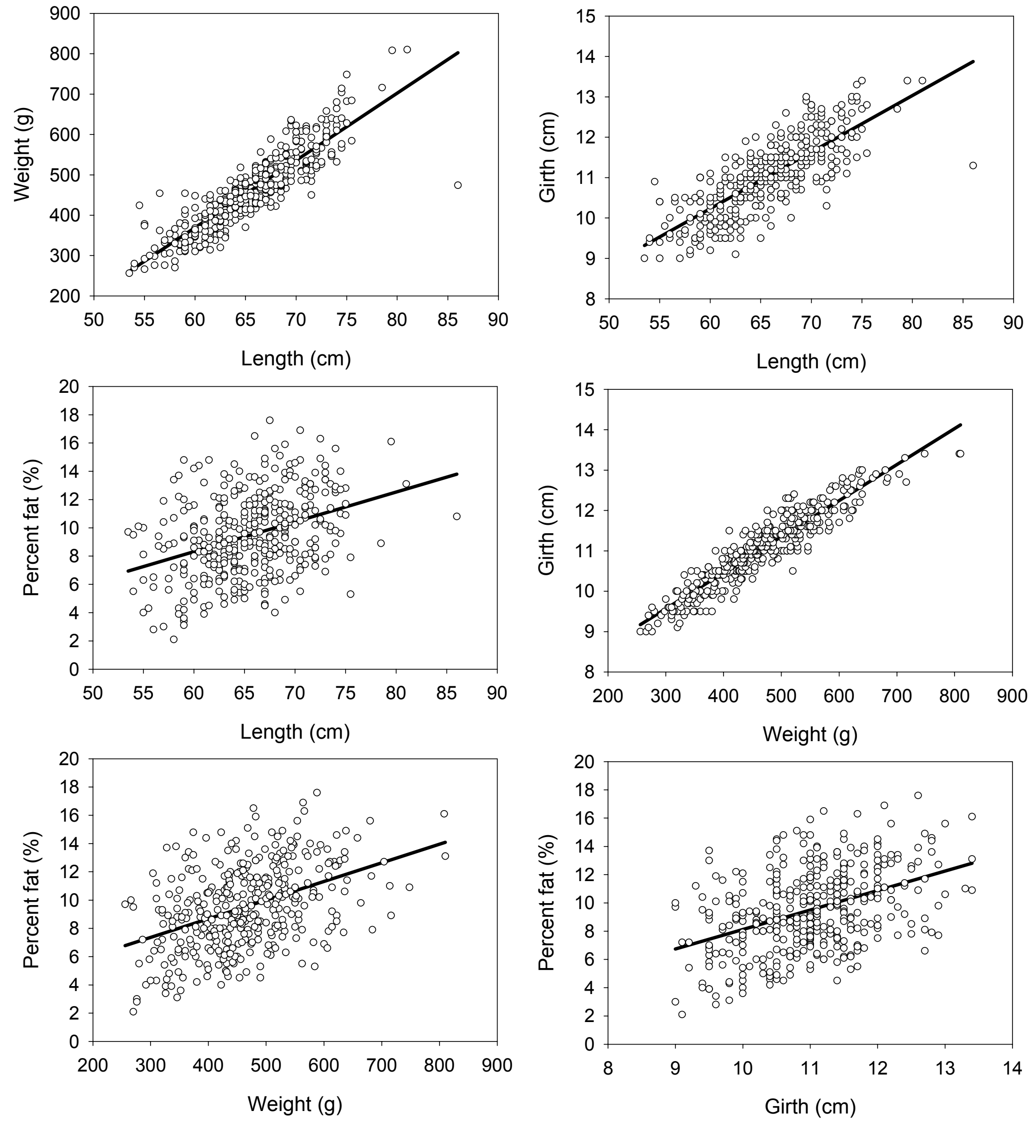

Figure 1. Linear relationships between length, weight, girth, and percent fat metrics for adult lamprey that were radio tagged in 2007.

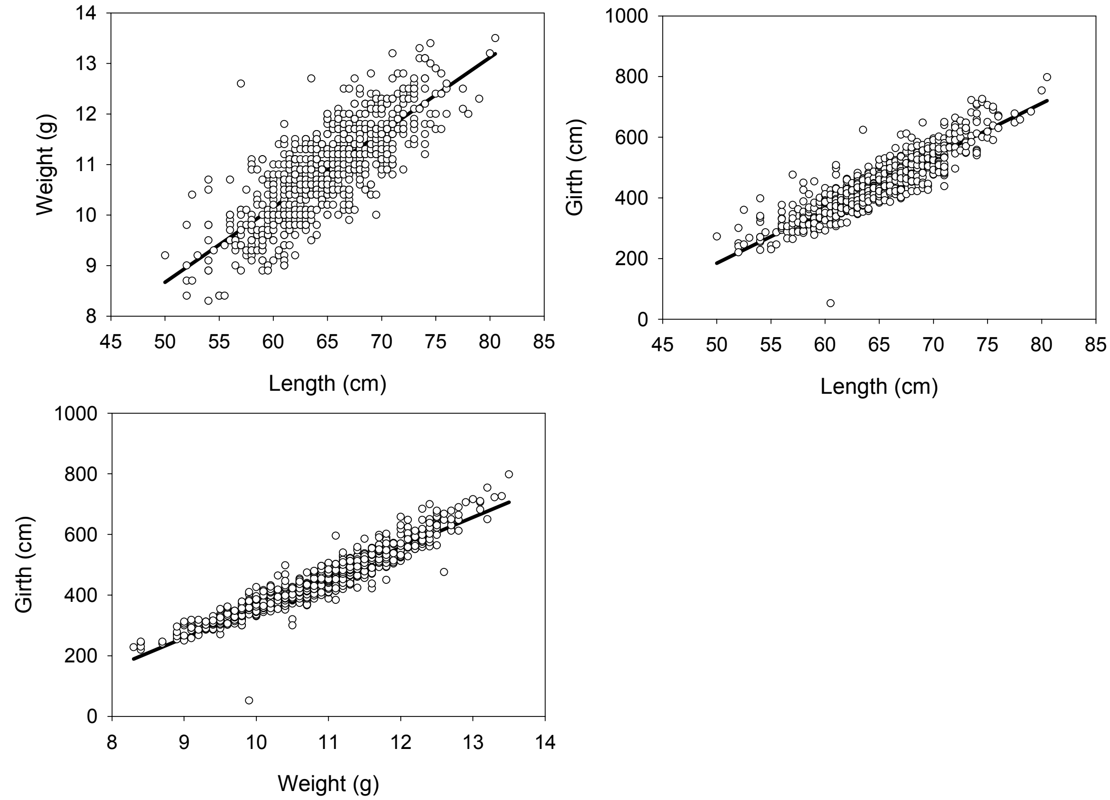

Figure 2. Linear relationships between length, weight, and girth metrics for adult lamprey that were HDX-PIT tagged in 2007.

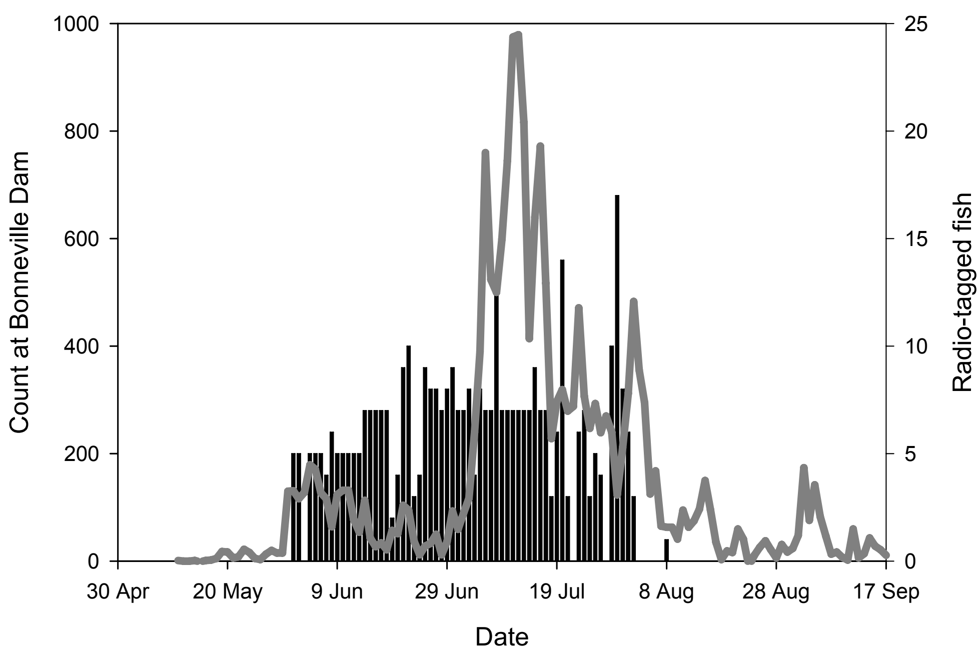

Figure 3. Number of adult Pacific lamprey counted passing Bonneville Dam via fish ladders (gray line) and the number that were collected and radio tagged (black bars, n = 398).

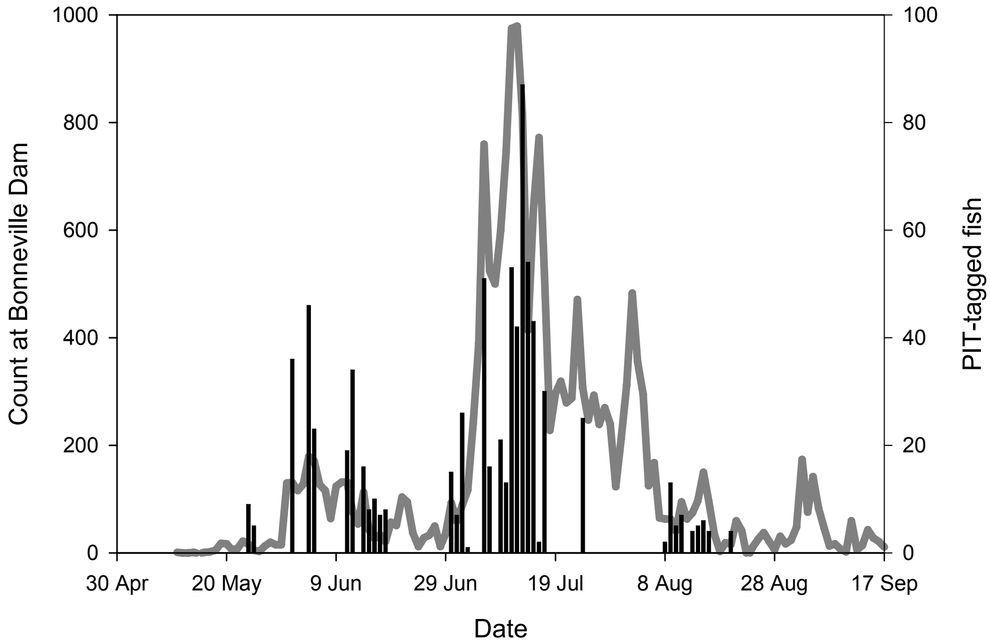

Figure 4. Number of adult Pacific lamprey counted passing Bonneville Dam via fish ladders (gray line) and the number that were collected and HDX-PIT tagged (black bars, *n* = 757).

Radiotelemetry

Upstream Progression – Of the 398 radio-tagged lamprey released downstream from Bonneville Dam, 271 (68.1%) were subsequently recorded at antennas at Bonneville Dam (excluding the aerial tailrace sites which potentially covered the release location) or at sites further upstream. A total of 83 fish passed the dam (20.9% of the 398 released, and 30.6% of the 271 detected at Bonneville antenna sites). The most upstream recorded locations for the 315 fish that did not pass the dam were: 127 (40%) in the tailrace only; 70 (22%) approaching fishway entrances; 85 (27%) inside fishways, collection channels, or transition pools; and 33 (10%) in the ladders either upstream from transition pools or at sites near the tops of ladders.

Fish that returned to the Bonneville fishways were slightly larger than fish that did not return. On average, returning fish were 0.6 cm longer, 19.7 g heavier, and had 0.2 cm wider girth, with the girth difference significant (P = 0.032, ANOVA) (Table 4). Returning fish were also tagged 3 d later, on average, than non-returning fish (P = 0.060), suggesting possible timing-related survival effects after release. Similarly, fish that passed the dam were larger than fish that were recorded at the dam but did not pass; these size differences were not statistically significant (length, P = 0.056; weight, P = 0.293; girth, P = 0.543).

The median tag date for all radio-tagged lampreys was 4 July. Median recorded passage dates at top-of-ladder sites were 13 July at Bonneville Dam (n = 71), 19 July at The Dalles Dam (n = 21), and 24 July at John Day Dam (n = 9). Top-of-ladder migration timing distributions for the radio-tagged fish approximated those for lamprey counts at the dams (Figure 5), though sample sizes were small at The Dalles and John Day dams.

Dam-to-Dam Escapement – Of 398 fish released, 20.9% (n = 83) were known to have passed Bonneville Dam, 5.3% (n = 21) passed The Dalles Dam, and 2.3% passed John Day Dam (Table 5). Conversion estimates from the top of Bonneville Dam were 25.3% to the top of The Dalles Dam and

10.8% to the top of John Day Dam. The conversion was 42.9% from the top of The Dalles Dam to the top of John Day Dam. Daily conversion estimates from release to the top of Bonneville Dam were quite variable, with no strong patterns evident (Figure 6).

In most cases, lampreys that successfully passed upstream sites were larger than those that did not pass (Table 4). Size differences were statistically significant ($P < 0.05$, ANOVA) for the reach from the release site to the top of Bonneville Dam (girth) and from release to the top of The Dalles Dam (length, weight, girth).

Table 4. Mean radio-tagged lamprey size metrics and tag dates in relation to their migration success through the monitored reaches in 2007. Top-of-ladder sites were used for the upper end of each reach. F and *P* values are from analysis of variance tests (ANOVA).

Reach	Passed	Length (*n*)	Weight (*n*)	Girth (*n*)	Tag date (*n*)
Release - Bonneville[1]	No	65.4 (127)	452.0 (127)	10.9 (127)	2 Jul (127)
	Yes	66.0 (270)	471.7 (271)	11.1 (269)	5 Jul (271)
	F	1.17	3.77	4.63	3.55
	P	0.280	0.053	0.032	0.060
Release - Bonneville top	No	65.5 (314)	461.4 (315)	11.0 (313)	4 Jul (315)
	Yes	66.9 (83)	480.8 (83)	11.2 (83)	30 Jun (83)
	F	4.76	2.79	1.76	2.78
	P	0.030	0.095	0.185	0.097
Release - The Dalles top	No	65.6 (376)	462.8 (377)	11.0 (375)	4 Jul (377)
	Yes	68.8 (21)	513.3 (21)	11.5 (21)	30 Jun (21)
	F	8.17	5.76	5.37	0.85
	P	0.005	0.017	0.021	0.358
Release - John Day top	No	65.7 (388)	464.6 (389)	11.0 (387)	4 Jul (389)
	Yes	68.6 (9)	501.3 (9)	11.5 (9)	30 Jun (9)
	F	2.81	1.33	1.92	0.37
	P	0.095	0.250	0.167	0.545
Bonneville top - The Dalles top	No	66.2 (62)	469.8 (62)	11.1 (62)	1 Jul (62)
	Yes	68.8 (21)	513.3 (21)	11.5 (21)	30 Jun (21)
	F	3.64	2.70	3.11	0.04
	P	0.060	0.104	0.082	0.840
The Dalles top - John Day top	No	69.0 (12)	522.3 (12)	11.5 (12)	91.3 (12)
	Yes	68.6 (9)	501.3 (9)	11.5 (9)	91.1 (9)
	F	0.07	0.40	0.03	0.00
	P	0.795	0.536	0.860	0.979

[1] not including tailrace antennas

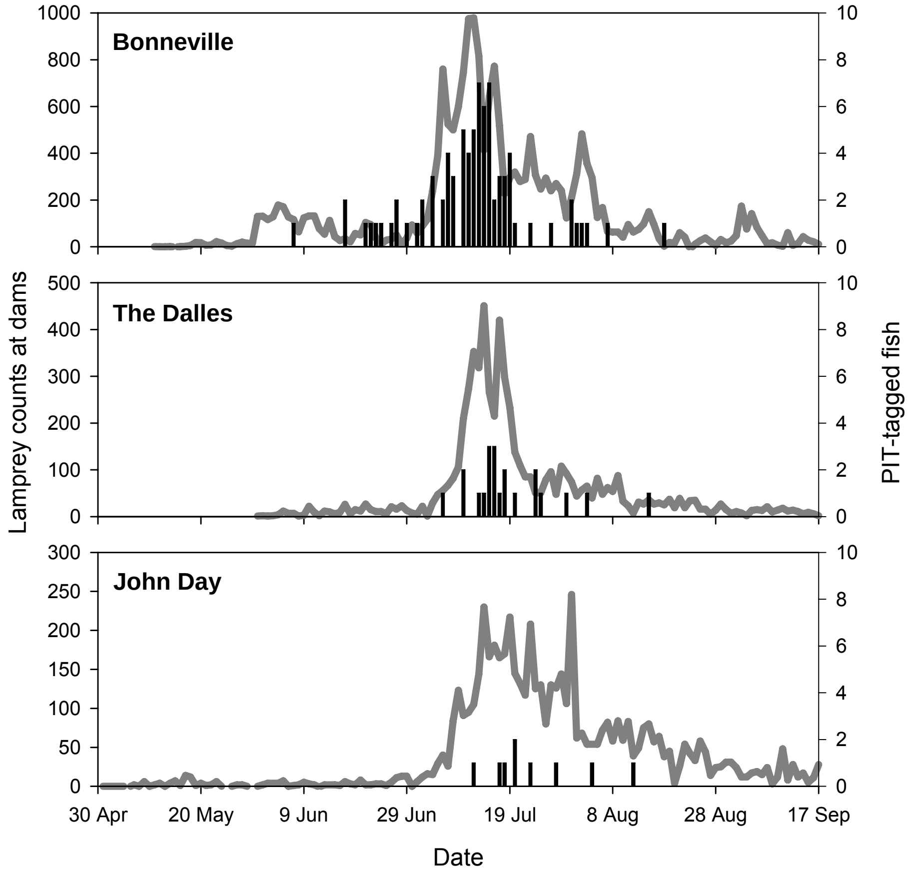

Figure 5. Daily numbers of adult Pacific lamprey counted passing dams via fish ladders (gray lines) and the numbers of radio-tagged fish that were detected at top-of-ladder radiotelemetry antennas (black bars) in 2007.

Passage Times and Rates – Median lamprey passage times were 7.6 d from the release site to the top of Bonneville Dam, 3.8 d between Bonneville and The Dalles dams, and 2.4 d between The Dalles and John Day dams (top-of-ladder sites at all dams, Table 6). Median passage rates (upstream migration distance divided by passage time in days) in these reaches were < 1 km•d^{-1} (release-Bonneville top), 19.2 km•d^{-1} (Bonneville-The Dalles), and 16.4 km•d^{-1} (The Dalles-John Day). Passage rates through reservoirs only (i.e., from ladder exit at the downstream dam to upstream dam tailrace) were 18.0 km•d^{-1} in the Bonneville reservoir and 26.2 km•d^{-1} in The Dalles reservoir.

Lamprey migration times from release to first approach and from release to first enter Bonneville Dam fishways were positively correlated (r = 0.13-0.15, P < 0.10) with lamprey size metrics (Table 7). In contrast, passage times from release to exit into the Bonneville Dam forebay were mostly uncorrelated with lamprey size but significantly (P < 0.10) decreased with migration date (r = -0.63) and water temperature (r = -0.68) and increased with flow (r = 0.43) (Figure 7). Passage times through the Bonneville-The Dalles and The Dalles-John Day reservoirs and between top-of-ladder sites were not significantly correlated with any tested variable (Table 7).

Median lamprey passage times through multiple dam-and-reservoir reaches were 14.7 d (5.2 km•d^{-1}) from release to the top of The Dalles Dam and 25.4 d (4.5 km•d^{-1}) from release to the top of John Day Dam (Table 6). In each case, times were negatively correlated with release date and water temperature (Table 7).

Table 5. Adult lamprey reach conversion estimates and detection efficiencies for radio-tagged fish in 2007. All estimates should be considered minimums. No fish were detected at any site upstream from John Day Dam. See Table 1 for antenna locations.

Site	Minimum past (*n*)	Detected (%)	Reach	Reach conversion (%)
Release	398		Release-Bonneville	68.1%
Bonneville[1]	271	100.0%	Release-Bonneville top	20.9%
Bonneville top[2]	83	85.5%	Release-The Dalles	9.5%
The Dalles[3]	38	100.0%	Release-The Dalles top	5.3%
The Dalles top[2]	21	100.0%	Release-John Day	2.8%
John Day[3]	11	100.0%	Release-John Day top	2.3%
John Day top[2]	9	100.0%		
			Bonneville-Bonneville top	30.6%
			Bonneville top-The Dalles top	25.3%
			Bonneville top-John Day top	10.8%
			The Dalles top-John Day top	42.9%

[1] all antennas, except tailrace
[2] top-of-ladder antennas
[3] all antennas, including tailrace

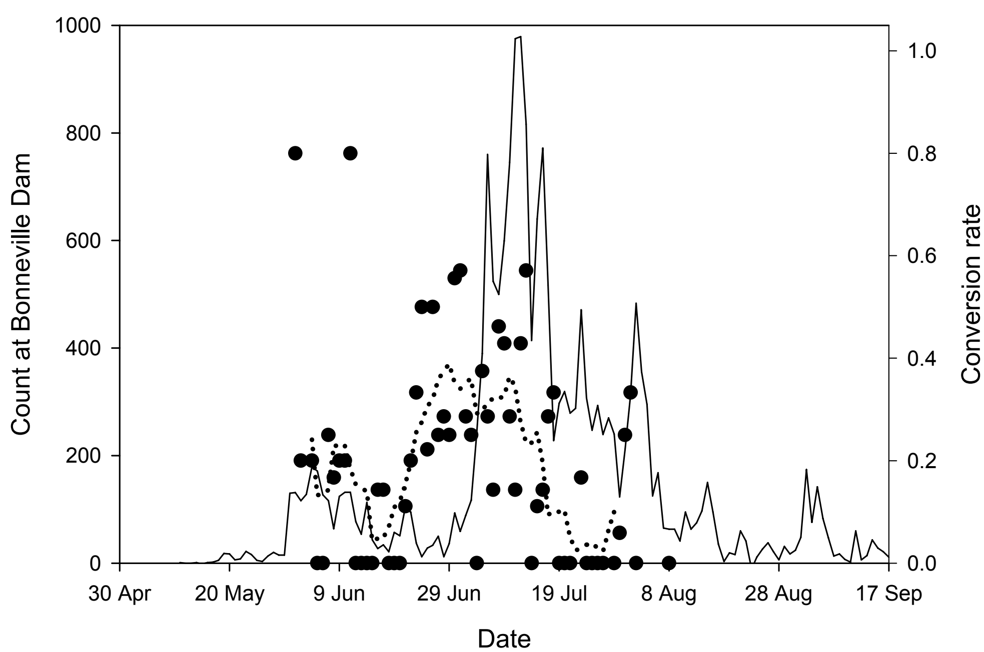

Figure 6. Daily radio-tagged lamprey conversion estimates (●) from release to the top of Bonneville Dam, by date of lamprey release near Hamilton Island in 2007. Dotted line shows 7-d moving average. Solid line shows daily counts of lamprey at the dam.

Table 6. Summary of radio-tagged adult lamprey passage times through dam-to-dam and multi-dam reaches of the lower Columbia River.

		Passage time (d)			
Reach	*n*	Median	Mean	Quartile 1	Quartile 3
Release to approach Bonneville fishway	266	3.12	7.59	0.62	7.32
Release to enter Bonneville fishway	176	3.97	10.66	0.98	9.50
Release to pass Bonneville Dam	71	7.56	11.28	2.69	14.99
Release to The Dalles tailrace	13	16.55	33.86	12.62	25.72
Release to pass The Dalles Dam	21	14.71	18.99	6.75	28.27
Release to John Day tailrace	7	17.06	20.43	14.52	27.03
Release to pass John Day Dam	9	25.38	24.19	14.45	34.17
Bonneville top to The Dalles tailrace	12	3.87	24.98	2.06	13.31
Bonneville top to pass The Dalles Dam	19	3.80	4.75	3.07	6.15
Bonneville top to John Day tailrace	6	4.22	6.03	3.59	5.30
Bonneville top to pass John Day Dam	7	6.04	7.67	4.71	8.74
The Dalles tailrace to pass The Dalles Dam	5	1.73	2.46	0.99	2.55
The Dalles top to John Day tailrace	7	1.41	2.87	0.97	1.66
The Dalles top to pass John Day Dam	9	2.36	3.74	1.84	3.70
John Day tailrace to pass John Day Dam	5	1.02	1.65	0.94	2.72

Table 7. Correlation coefficients (*r*) for log-transformed radio-tagged lamprey passage times (d) in 2007. Predictor variables included size metrics (length, weight, girth) recorded at the time of tagging and date, and Columbia River flow and temperature on the date fish were released or passed the top-of-ladder sites at Bonneville or The Dalles dams for each reach. Gray shading indicates $P < 0.05$.

			Correlation coefficient (*r*)					
Reach start	Reach end	*n*	Length	Weight	Girth	Date	Flow	Temp.
Release	Bonneville approach	266	0.13	0.13	0.13	-0.02	-0.03	-0.08
Release	Bonneville entry	176	0.14	0.15	0.13	-0.10	0.03	-0.13
Release	Bonneville top	71	-0.01	-0.00	0.02	-0.63	0.43	-0.68
Release	The Dalles tailrace	13	-0.13	0.03	0.09	-0.33	0.20	-0.38
Release	The Dalles top	21	-0.29	-0.08	0.17	-0.72	0.42	-0.75
Release	John Day tailrace	7	0.09	0.51	0.79	-0.64	0.74	-0.62
Release	John Day top	9	-0.16	0.04	0.33	-0.67	0.48	-0.67
Bonneville top	The Dalles tailrace	12	-0.30	-0.13	0.18	-0.06	-0.36	-0.34
Bonneville top	The Dalles top	19	-0.02	-0.08	-0.05	-0.33	-0.20	-0.07
Bonneville top	John Day tailrace	6	-0.08	-0.15	0.19	-0.40	-0.78	-0.39
Bonneville top	John Day top	7	-0.41	-0.29	-0.29	-0.53	-0.94	-0.54
The Dalles top	John Day tailrace	7	0.09	0.05	0.10	-0.42	0.45	-0.37
The Dalles top	John Day top	9	0.37	0.50	0.61	0.46	-0.25	0.10

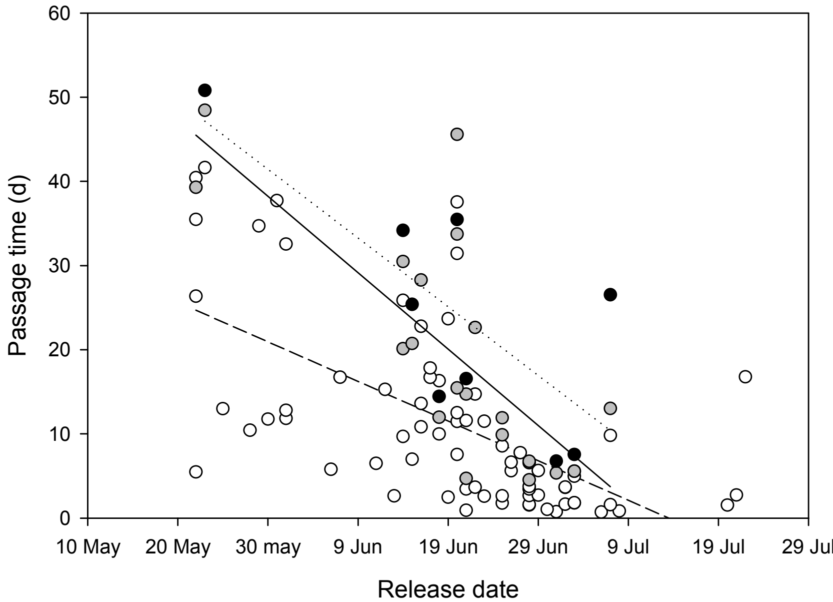

Figure 7. Radio-tagged lamprey migration times from release below Bonneville Dam to the ladder exit sites at Bonneville (○, dashed line), The Dalles (●, solid line), and John Day (●, dotted line) dams in 2007. Lines show linear regression relationships.

Diel Passage – Lamprey passage distributions at top-of-ladder sites clearly showed that most passage occurred at night (Figure 8). This pattern was consistent at the three lower Columbia River dams. The majority of passage events were between sunrise and sunset, though some fish passed during almost all hours. Daylight passage most often occurred between 0500 and 1100, suggesting that some fish that initiated dam passage at night may have continued migrating in the morning in an effort to exit fishways.

Detection Efficiency – Broad-scale detection efficiencies for the radio-tagged fish at Bonneville, The Dalles, and John Day dams indicated that fish that reached the dams were likely to be detected on one or more antennas (Table 4). At Bonneville Dam, 391 fish were recorded at one or more sites. Of these, 380 (96.4%) were detected on aerial tailrace antennas. A total of 271 fish were recorded at antennas upstream from the Bonneville tailrace (including approaching fishways) and 201 were recorded inside Bonneville fishways. Of the 201 recorded inside fishways, 177 (88.1%) were recorded passing an entrance antenna; the entry detection efficiency may have been slightly higher than 88.1% because fish could enter unmonitored orifice gates at Powerhouse II. A minimum of 83 lamprey were known to pass Bonneville Dam, of which 71 (85.5%) were detected at top-of-ladder antennas. Eight of the 12 that were not recorded passing top-of-ladder sites were last detected at antennas in the auxiliary channel near the lamprey bypass system at the top of the Bradford Island ladder; because these fish may have passed the dam via the bypass, this result suggests overall detection efficiencies were likely higher than 85.5%.

A total of 38 fish were detected at The Dalles Dam. Seventeen of the 38 (44.7%) were recorded on aerial tailrace antennas. Thirty-one fish were recorded at antennas monitoring fishway entrances or inside fishways. Twenty-nine were recorded inside fishways, of which 25 (86.2%) were recorded passing fishway entrance antennas. Twenty-two fish were known to pass The Dalles Dam, and all were recorded at top-of-ladder antennas (Table 4).

Eleven lamprey were recorded at John Day Dam antennas, with seven (63.6%) recorded on aerial tailrace antennas. The only additional antennas at John Day Dam were at the top-of-ladder sites, where nine fish were recorded. No fish were recorded at McNary Dam.

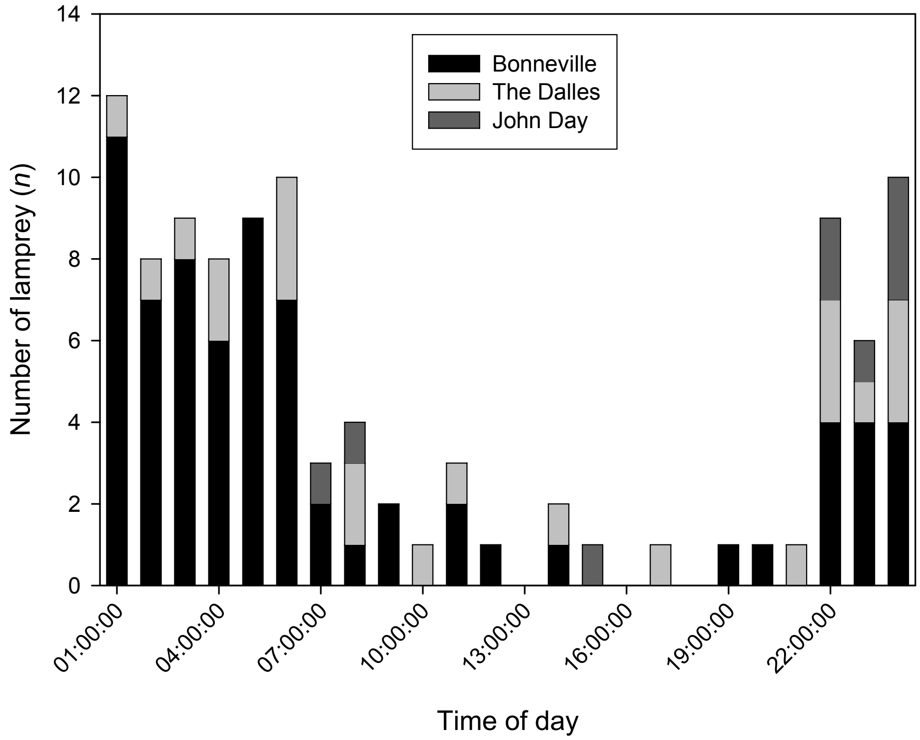

Figure 8. Distributions of the times that radio-tagged lamprey were detected passing top-of-ladder sites at Bonneville, The Dalles, and John Day dams in 2007.

Half-Duplex PIT Tag

Upstream Progression – Of the 757 HDX-PIT tagged lampreys released downstream from Bonneville Dam, 476 (62.9%) were subsequently recorded at the antenna used to monitor the Washington-shore fishway entrance, at antennas inside Bonneville Dam fishways (i.e., above the Washington-shore transition pool or near top-of-ladder sites), or at dams further upstream. A total of 383 fish passed the dam (50.6% of the 757 released, and 82.6% of the 476 detected at Bonneville antenna sites).

The median tag date for all HDX-PIT tagged lamprey was 11 July. Median recorded passage dates at top-of-ladder sites were 16 July at Bonneville Dam (*n* = 340), 22 July at The Dalles Dam (*n* = 200), 29 July at John Day Dam (*n* = 126), and 5 August at McNary Dam (*n* = 33). Top-of-ladder migration timing distributions for the HDX-PIT tagged fish indicated relative under-sampling during migration peaks, but with tagged fish present through most of the run at all dams (Figure 9).

Dam-to-Dam Escapement – Of 757 fish released, 62.9% (*n* = 393) were known to have passed Bonneville Dam, 32.5 % (*n* = 247) passed The Dalles Dam, 17.0% (*n* = 129) passed John Day Dam, and 4.6% (*n* = 35) passed McNary Dam (Table 8). Conversion estimates from the top of Bonneville Dam were 62.8% to the top of The Dalles Dam, 32.8% to the top of John Day Dam, and 8.9% to the top of McNary Dam. Conversions were 52.2% between ladder tops at The Dalles Dam and John Day dams and 27.1% between ladder tops at John Day to McNary dams. Five lamprey were recorded passing Ice Harbor Dam, representing 0.7% of the total sample and 14.3% of the fish that passed McNary Dam (Table 8). Conversion rates between dams were variable through time, but did not appear to have strong seasonal patterns (Table 9 and Figure 10).

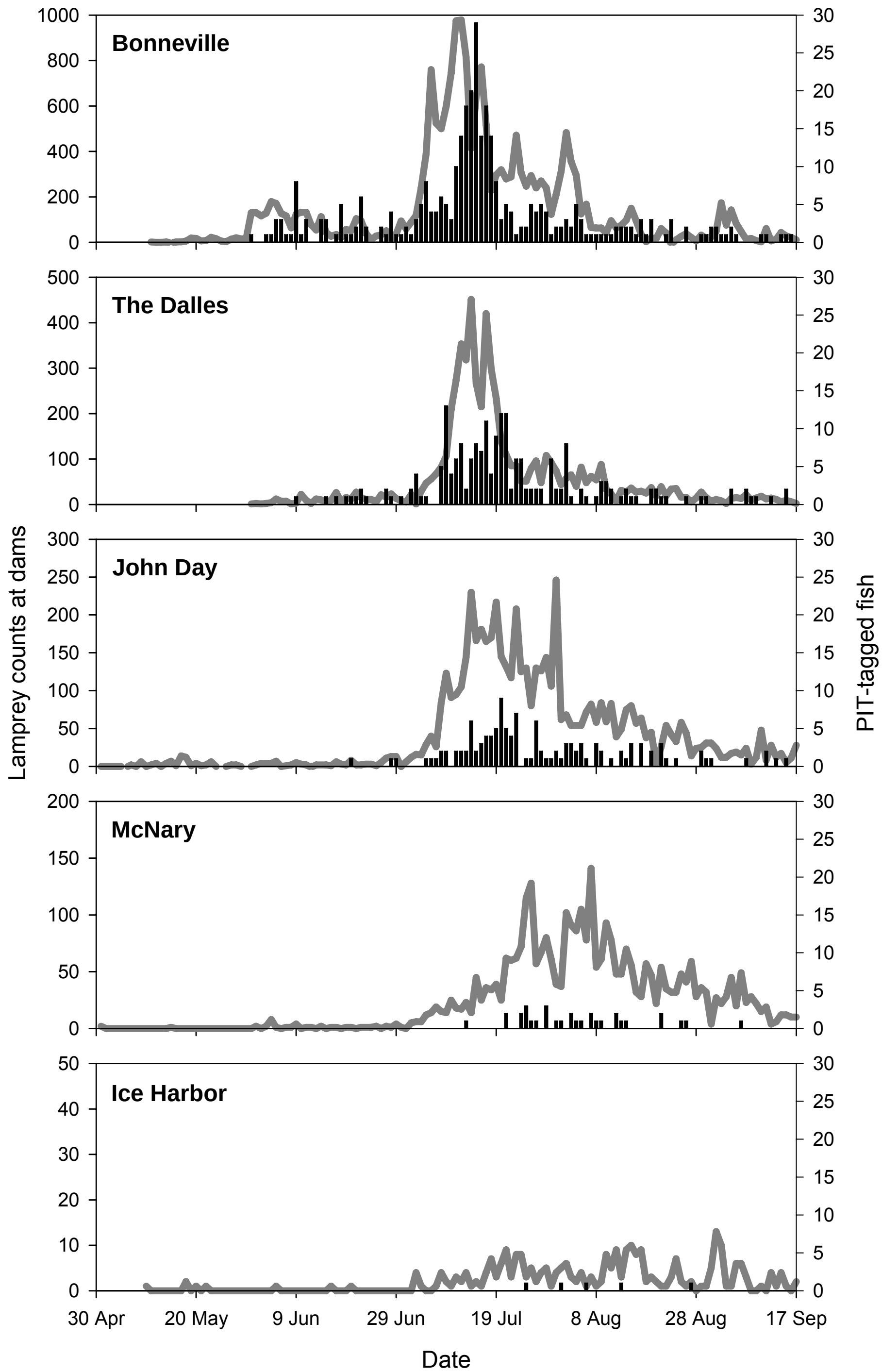

Figure 9. Daily numbers of adult Pacific lamprey counted passing dams via fish ladders (gray lines) and the numbers of HDX-PIT tagged fish that were detected at top-of-ladder antennas (black bars) in 2007.

Table 8. Adult HDX-PIT tagged lamprey reach conversion estimates for 2007. All estimates should be considered minimums. See Table 2 for antenna locations.

Site	Minimum past (*n*)	Detected (%)	Reach conversion Reach	(%)
Release	757		Release-Bonneville	62.9%
Bonneville[1]	476	93.7%	Release-Bonneville top	51.9%
Bonneville top[2]	393	86.5%	Release-The Dalles	37.1%
The Dalles[1]	281	96.1%	Release-The Dalles top	32.5%
The Dalles top[2]	247	81.7%	Release-John Day top	17.0%
John Day top[2]	129	97.7%	Release-McNary	6.9%
McNary[1]	52	100.0%	Release-McNary top	4.6%
McNary top[2]	35	94.3%	Release-Ice Harbor	1.1%
Ice Harbor[1]	8	100.0%	Release-Ice Harbor top	0.7%
Ice Harbor top[2,4]	5	100.0%		
			Bonneville-Bonneville top	82.6%
			Bonneville top-The Dalles top	62.8%
			Bonneville top-John Day top	32.8%
			Bonneville top-McNary top	8.9%
			Bonneville top-ice Harbor top	1.3%
			The Dalles top-John Day top	52.2%
			The Dalles top-McNary top	14.2%
			The Dalles top-Ice Harbor top	2.0%
			John Day top-McNary top	27.1%
			John Day top-Ice Harbor top	3.9%
			McNary top-Ice Harbor top	14.3%

[1] all fishway antennas, including LPS at Bonneville
[2] top-of-ladder antennas, including LPS at Bonneville
[3] all antennas, including tailrace
[4] No upstream site to assess missed detections

Table 9. Dam-to-dam lamprey conversion rates, calculated from the date fish were released or when they were recorded at top-of-ladder sites at dams. Fish that passed undetected at the downstream end of each reach were excluded. BO = Bonneville, TD = The Dalles, JD = John Day, MN = McNary.

	Conversion estimate							
	Release - BO top		BO top - TD top		TD top - JD top		JD top - MN top	
Block	*n*	%	*n*	%	*n*	%	*n*	%
24 May-3 Jun	52	52.0	2	50.0				
4 Jun-13 Jun	122	45.1	21	23.8	1	100.0		
14 Jun-23 Jun	49	51.0	24	54.2	8	25.0	1	0.0
24 Jun-3 Jul	49	63.3	15	33.3	10	30.0	2	0.0
4 Jul-13 Jul	282	57.5	77	71.4	37	46.0	13	30.8
14 Jul-23 Jul	129	47.3	116	61.3	77	44.2	49	36.7
24 Jul-2 Aug	25	40.0	30	70.0	32	34.4	18	33.3
3 Aug-12 Aug	27	44.4	18	50.0	13	61.5	15	13.3
13 Aug-22 Aug	23	47.8	15	60.0	11	27.3	15	13.3
23 Aug-1 Sep			22	40.9	12	41.7	13	15.4

In almost all reaches, lamprey that successfully passed upstream sites were significantly ($P < 0.05$) larger than those that did not pass (Table 10). In contrast, passage success was not significantly associated with the date that lamprey were released downstream from Bonneville Dam. For the most part, mean dates that successful and unsuccessful lamprey passed upstream antenna sites were not statistically associated with eventual dam-to-dam conversion, with the largest difference between groups (7 d, P = 0.076) at John Day Dam (Table 11). Temperature and flow conditions lamprey encountered on the dates they entered upstream reaches did not significantly differ between fish that did or did not pass the next upstream dam, with one exception: lamprey that passed McNary Dam encountered higher flow at John Day Dam than those that did not pass McNary Dam (Table 11, P = 0.021). This finding was consistent with the finding that fish successfully passing McNary Dam were generally detected earlier in the season at John Day Dam than those fish that were unsuccessful.

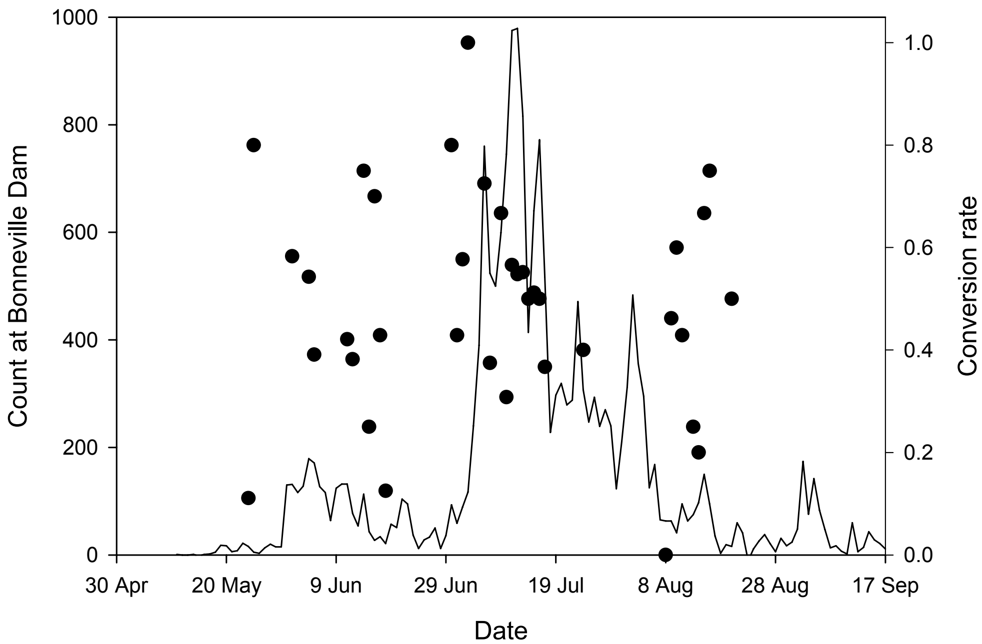

Figure 10. Daily HDX-PIT tagged lamprey conversion estimates (●) from release to the top of Bonneville Dam, by date of lamprey release in 2007. Solid line shows daily counts of lamprey at the dam.

Passage Times and Rates – Median HDX-PIT tagged lamprey passage times were 6.5 d from the release site to the top of Bonneville Dam, 4.0 d between Bonneville and The Dalles dams, 4.3 d between The Dalles and John Day dams, and 8.8 d between John Day and McNary dams (top-of-ladder sites at all dams, Table 12). Median passage rates in these reaches were < 1 km•d^{-1} (release-Bonneville top), 18.3 km•d^{-1} (Bonneville-The Dalles), 9.7 km•d^{-1} (The Dalles-John Day), and 14.0 km•d^{-1} (John Day-McNary). Rates over multi-dam reaches were: 12.3 km•d^{-1} (Bonneville-John Day), 13.7 km•d^{-1} (Bonneville-McNary), and 13.6 km•d^{-1} (The Dalles-McNary).

Lamprey migration times were correlated with fish size metrics, migration dates, and river environment variables (Table 13). These variables were inter-related, as flow decreased and temperature increased with date and fish were slightly larger earlier in the season. In general passage times were positively correlated with river flow (i.e., slower migration rates at higher flow, Figure 11) and were negatively correlated with migration date and temperature (i.e., faster migration rates as temperatures rose). Larger fish tended to have slower passage times, especially through reaches that started at the release site, perhaps reflecting higher flow and cooler temperatures fish encountered early in the migration (Table 13). Overall, however, the selected predictor variables explained relatively small proportions of the variability in lamprey passage times; the highest correlation coefficients were for environmental metrics over multi-dam reaches.

Table 10. Mean HDX-PIT tagged lamprey size metrics and tag/migration dates in relation to their migration success through the monitored reaches in 2007. Top-of-ladder sites were used for the upper end of each reach. F and *P* values are from analysis of variance tests (ANOVA).

Reach	Passed	Length (*n*)	Weight (*n*)	Girth (*n*)	Tag date (*n*)
Release - Bonneville top	No	64.3 (363)	435.1 (363)	10.8 (364)	4 Jul (364)
	Yes	65.3 (393)	453.7 (393)	11.0 (393)	4 Jul (393)
	F	6.74	6.91	9.84	0.00
	P	0.010	0.009	0.002	0.950
Release - The Dalles top	No	64.2 (509)	430.8 (509)	10.7 (510)	3 Jul (510)
	Yes	66.1 (247)	473.6 (247)	11.2 (247)	4 Jul (247)
	F	26.56	33.43	42.19	0.28
	P	<0.001	<0.001	<0.001	0.598
Release - John Day top	No	65.7 (388)	432.0 (627)	10.7 (628)	4 Jul (389)
	Yes	68.6 (129)	507.0 (129)	11.5 (129)	4 Jul (9)
	F	45.43	69.24	79.50	0.00
	P	<0.001	<0.001	<0.001	0.980
Release - McNary top	No	64.6 (721)	440.4 (721)	10.8 (722)	4 Jul (389)
	Yes	68.4 (35)	535.8 (35)	11.8 (35)	2 Jul (9)
	F	19.28	33.43	34.90	0.40
	P	<0.001	<0.001	<0.001	0.527
Bonneville top - The Dalles top	No	63.8 (147)	420.8 (147)	10.6 (147)	3 Jul (147)
	Yes	66.1 (246)	473.3 (246)	11.2 (246)	4 Jul (247)
	F	23.38	28.49	34.79	0.47
	P	<0.001	<0.001	<0.001	0.492
Bonneville top - John Day top	No	64.2 (264)	427.7 (264)	10.7 (264)	4 Jul (12)
	Yes	67.5 (129)	507.0 (129)	11.5 (129)	4 Jul (9)
	F	45.10	66.77	76.96	0.00
	P	<0.001	<0.001	<0.001	0.998
Bonneville top - McNary top	No	64.9 (358)	445.7 (358)	10.9 (358)	4 Jul (358)
	Yes	68.4 (35)	535.8 (35)	11.8 (35)	2 Jul (35)
	F	17.51	29.07	30.31	0.47
	P	<0.001	<0.001	<0.001	0.492
The Dalles top - John Day top	No	64.7 (118)	437.0 (118)	10.8 (118)	5 Jul (119)
	Yes	67.5 (129)	507.0 (129)	11.5 (129)	4 Jul (128)
	F	23.20	36.72	44.29	0.21
	P	<0.001	<0.001	<0.001	0.646
The Dalles top - McNary top	No	65.8 (212)	463.3 (212)	11.1 (212)	5 Jul (212)
	Yes	68.4 (35)	535.8 (35)	11.8 (35)	2 Jul (35)
	F	10.00	17.92	19.39	0.86
	P	0.002	<0.001	<0.001	0.355
John Day top - McNary top	No	67.1 (94)	496.3 (94)	11.4 (94)	4 Jul (94)
	Yes	68.4 (35)	535.8 (35)	11.8 (35)	2 Jul (35)
	F	2.12	4.38	4.83	0.61
	P	0.148	0.038	0.030	0.438

Table 11. Mean HDX-PIT tagged lamprey migration dates and encountered water temperature and discharge in relation to their migration success through the monitored reaches in 2007. Environmental data were from the dates fish were recorded passing the lower end of each reach. Top-of-ladder sites were used for the upper end of each reach. F and *P* values are from analysis of variance tests (ANOVA).

Reach	Passed	Date (*n*)	Temperature (*n*)	Flow (*n*)
Release - Bonneville top	No	4 Jul (364)	18.97 (364)	200.4 (364)
	Yes	4 Jul (393)	19.02 (393)	199.0 (393)
	F	0.00	0.12	0.40
	P	0.950	0.731	0.529
Bonneville top - The Dalles top	No	16 Jul (143)	19.75 (140)	185.2 (143)
	Yes	17 Jul (197)	20.20 (197)	181.9 (197)
	F	0.25	5.29	0.73
	P	0.618	0.022	0.394
The Dalles top - John Day top	No	22 Jul (117)	20.54 (118)	161.2 (118)
	Yes	22 Jul (84)	20.62 (85)	161.1 (85)
	F	0.00	0.22	0.00
	P	0.975	0.641	0.979
John Day top - McNary top	No	1 Aug (92)	20.90 (92)	153.5 (92)
	Yes	25 Jul (34)	21.02 (34)	166.7 (34)
	F	3.21	0.57	5.44
	P	0.076	0.450	0.021

Table 12. Summary of HDX-PIT tagged adult lamprey passage times through monitored reaches of the lower Columbia River.

		Passage time (d)			
Reach	*n*	Median	Mean	Quartile 1	Quartile 3
Release to pass Bonneville Dam	340	6.48	12.84	2.61	18.49
Release to pass The Dalles Dam	200	11.69	17.55	6.51	24.93
Release to pass John Day Dam	126	21.49	26.16	11.56	36.49
Release to pass McNary Dam	33	30.70	33.40	18.01	48.25
Release to pass Ice Harbor Dam	5	54.74	44.25	25.76	57.65
Bonneville top to pass The Dalles Dam	156	4.04	6.05	2.78	8.12
Bonneville top to pass John Day Dam	109	9.07	12.55	5.77	14.02
Bonneville top to pass McNary Dam	31	17.09	19.29	12.31	22.53
Bonneville top to pass Ice Harbor Dam	4	34.28	35.14	28.46	40.96
The Dalles top to pass John Day Dam	82	4.31	7.60	2.96	7.89
The Dalles top to pass McNary Dam	20	11.85	15.86	9.83	19.84
The Dalles top to pass Ice Harbor Dam	4	22.05	27.80	18.47	31.38
John Day top to pass McNary Dam	32	8.81	11.44	6.47	12.33
John Day top to pass Ice Harbor Dam	5	17.28	23.68	13.24	29.33
McNary top to pass Ice Harbor Dam	3	15.77	14.38	9.56	19.90

Diel Passage – As with the telemetry data, lamprey passage distributions at top-of-ladder sites clearly showed that most dam passage occurred at night (Figure 12). This pattern was consistent across the four lower Columbia River dams. The majority of passage events were between sunrise and sunset, though some fish passed during all hours.

Table 13. Correlation coefficients (r) for log-transformed HDX-PIT tagged lamprey passage times (d) in 2007. Predictor variables included size metrics (length, weight, girth) recorded at the time of tagging and date, Columbia River flow, and temperature at the downstream site for each reach. Gray shading indicates $P < 0.05$.

			Correlation coefficient (r)					
Reach start	Reach end	n	Length	Weight	Girth	Date	Flow	Temp.
Release	Bonneville top	340	0.201	0.224	0.210	-0.319	0.244	-0.382
Release	The Dalles top	200	0.183	0.220	0.200	-0.420	0.412	-0.432
Release	John Day top	126	0.135	0.180	0.188	-0.452	0.395	-0.467
Release	McNary top	33	0.316	0.395	0.388	-0.632	0.615	-0.574
Bonneville top	The Dalles top	156	-0.078	-0.079	-0.068	-0.069	-0.009	-0.270
Bonneville top	John Day top	109	-0.088	-0.109	-0.047	-0.099	0.044	-0.253
Bonneville top	McNary top	31	0.166	0.199	0.231	-0.257	-0.071	-0.383
The Dalles top	John Day top	82	-0.136	-0.081	-0.023	-0.030	0.079	-0.092
The Dalles top	McNary top	20	-0.081	-0.102	-0.029	-0.401	-0.020	-0.577
John Day top	McNary top	32	0.168	0.166	0.185	-0.249	0.342	-0.290

Detection Efficiency – Estimating detection efficiencies for the HDX-PIT sites was difficult due to a lack of antenna redundancy in individual fishways and lamprey passage structures (Bonneville only). A total of 476 lampreys were either recorded at Bonneville detection antennas or passed the dam and were detected at upstream dams. Of the 476, 446 (93.7%) were detected on a Bonneville HDX-PIT antenna (Table 8). A total of 393 lamprey were recorded passing Bonneville Dam or were recorded at upstream sites. Of these, 340 (86.5%) were detected at top-of-ladder antennas or in lamprey passage systems where exit to the forebay was likely. Of the 53 fish that passed Bonneville Dam without detection at an exit site, 23 (43.4%) were recorded on antennas in the Washington-shore or Cascades Island fishways and 30 (56.6%) were not detected at any site. It was not possible to determine if these fish passed undetected or via unmonitored routes (e.g., the navigation lock or UMT channel).

A total of 281 lamprey were detected at HDX-PIT antennas at The Dalles Dam or at sites upstream from The Dalles. Of the 281, 270 (96.1%) were detected at The Dalles antennas. A total of 247 fish were known to have passed The Dalles Dam, of which 201 (81.7%) were detected at top-of-ladder antennas. Of the 46 fish that passed but were not recorded at top-of-ladder antennas, 33 (71.7%) were recorded at an antenna above the count window in the East ladder.

At John Day Dam, 126 of 129 lamprey (97.7%) known to pass the dam were detected at John Day Dam top-of-ladder antennas.

At McNary Dam, 52 fish were detected at HDX-PIT antennas; no additional fish were detected upstream at Ice Harbor Dam (Table 8). Thirty-five lamprey passed McNary Dam, of which 33 (94.3%) were detected at top-of-ladder antennas. The two fish not recorded at the exit sites were detected at the antenna in the Washington-shore transition pool area. Ten fish were recorded exiting via the Washington-shore ladder, of which 4 (40.0%) were also detected at the Washington-shore transition pool antenna. Twenty-five fish were recorded exiting the Oregon-shore ladder, and 21 (84.0%) were also recorded at the antennas in the Oregon-shore transition pool area.

Eight lamprey were detected at Ice Harbor HDX-PIT antennas, with five recorded at top-of-ladder sites (Table 8). The five that passed were also detected at antennas near fishway entrances and/or in transition pools.

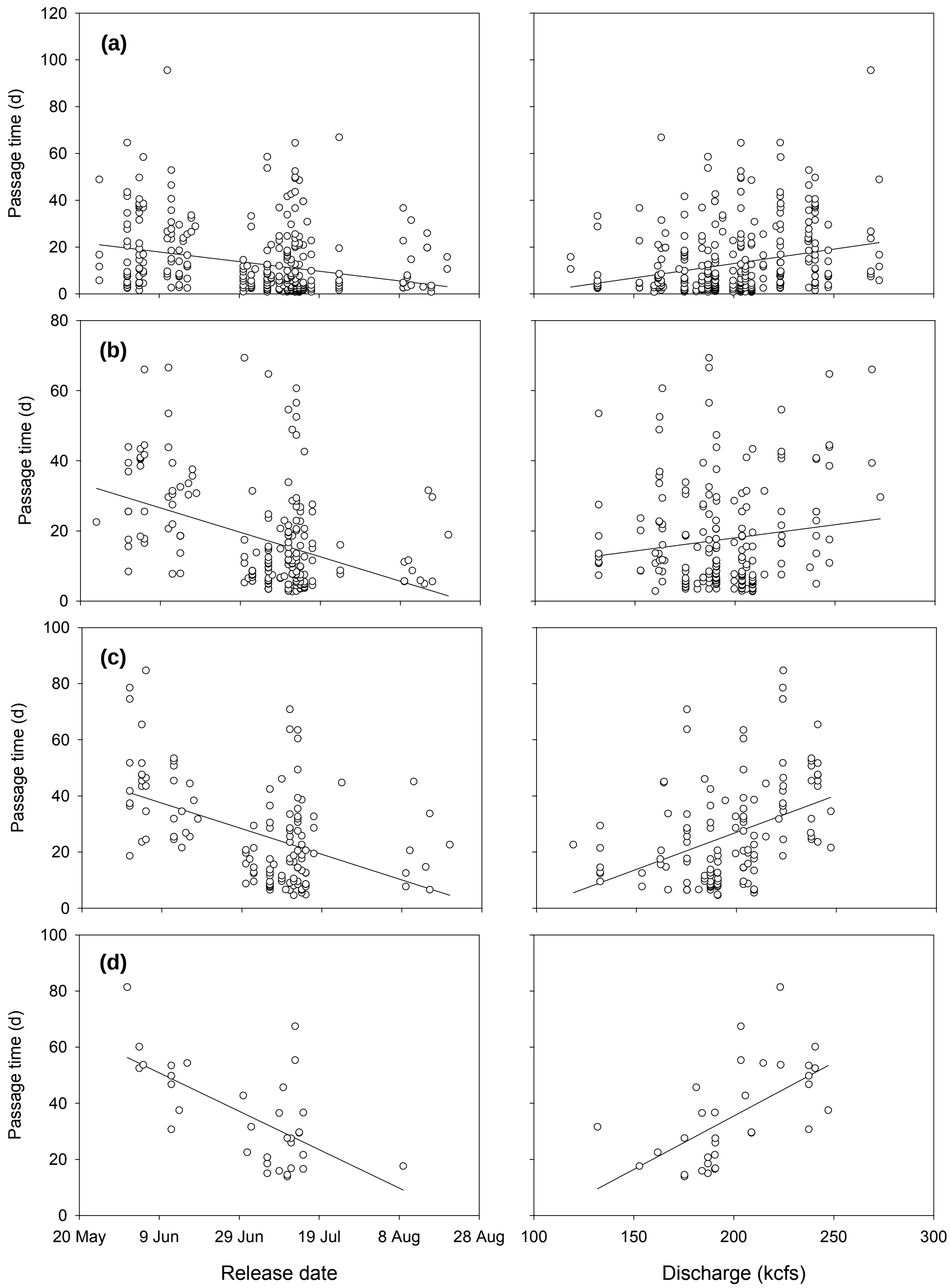

Figure 11. Linear regressions showing relationships between HDX-PIT tagged lamprey migration times (d) from release below Bonneville Dam to the ladder exit sites at Bonneville, The Dalles, John Day, and McNary dams and release date and total Columbia River discharge in 2007. Lines show linear regression relationships. Correlation coefficients in Table 13.

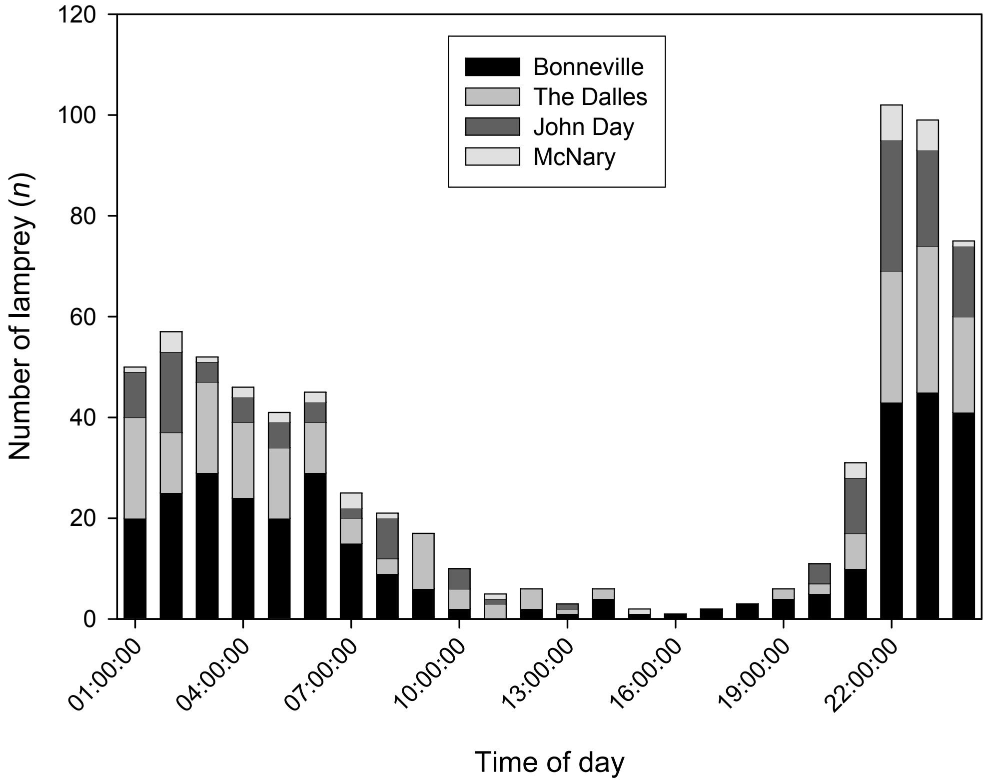

Figure 12. Distributions of the times that HD PIT-tagged lamprey were detected passing top-of-ladder sites at Bonneville, The Dalles, John Day, and McNary dams in 2007.

Discussion

Comparison of Results by Tag Type

A concern in the 2007 studies was that radio-tagged fish had lower reach conversion estimates than HDX-PIT tagged fish through all study reaches (see Tables 5 and 8). In contrast, passage times for the two groups were generally similar, with radio-tagged fish passing more rapidly in some reaches and HDX-PIT tagged fish passing faster in others (Tables 6 and 9). Other patterns, such as higher conversion estimates for larger fish, were also consistent across tag types.

Plausible explanations for the conversion differences between methods include: 1) tag effects (e.g., radio transmitters negatively affected survival), 2) transmitter problems (e.g., battery or transmission failure), 3) poor detection efficiencies at telemetry antennas, 4) effects of different tagging schedules between tag types, or 5) a combination of effects.

In preparation for the 2007 studies we recommended that some fish should have been double tagged with HDX-PIT and radio tags to crosscheck the performance of both tag types. However, double-tagging was eliminated in an effort to keep radiotelemetry results as comparable as possible to previous studies. As a result, we could only attempt to rule out potential explanations for the relative underperformance of radio-tagged fish by using an *ex post facto* series of tests. First, we tested for tag effects by comparing logistic regression models that included tag type, tag date, and fish weight predictor variables in various combinations (Burnham and Anderson 2002). Using AIC, the model that included tag type and fish weight was the most parsimonious (Table 14). In this model, HDX-PIT tagged fish were 4.3 times (odds ratio: 95% ci = 3.3-5.8) more likely than radio-tagged fish to pass Bonneville Dam (χ^2 = 101.8, P < 0.0001). In addition, larger fish were significantly more likely to pass the dam across both tag types (χ^2 = 9.5, P = 0.0020). Importantly, this model adjusted for the larger mean size of radio-tagged fish (~ 1 cm and 20 g). Models that included tag date and/or weight — but not tag type — explained much smaller portions of the variability in conversion past Bonneville Dam (Table 14). These results implicate either a negative radio-tagging effect or a problem with the transmitters and/or detections on fishway antennas.

In a separate effort to address the question of low detection efficiencies we compared the number of records per radio-tagged fish at individual antennas at Bonneville Dam in 2007 to similar record counts for fish radio-tagged in 2002. This analysis indicated that detection numbers were widely variable across fish and antenna sites in both years. However, we found no consistent pattern of lower detections in the 2007 sample. This suggests that transmitters performed similarly in each year, but does not rule out the possibility that some transmitters failed in the 2007 study. The majority of the radio-tagged fish that did not pass Bonneville Dam (n = 315) were last recorded in the tailrace (40%) or approached but did not enter fishways (22%). These results provide some spatial resolution on the unsuccessful fish but do not resolve the cause for relatively low success for radio-tagged fish.

Table 14. Model comparison results for logistic regression models where the dependent variable was successful passage of Bonneville Dam and independent variables were tagtype (radio, HDX-PIT), tagdate, and fish weight (g). ΔAIC = the change in AIC relative to the most parsimonious model.

Model	*df*	AIC	ΔAIC
Tagtype + Weight	**2**	**1450.8**	**0.0**
Tagtype + Tagdate + Weight	3	1452.7	1.9
Tagtype×Weight	1	1457.2	6.4
Tagtype	1	1459.9	9.1
Tagtype + Tagdate	2	1461.4	10.6
Tagtype×Tagdate	1	1464.7	13.9
Weight	1	1564.6	113.8
Tagdate + Weight	2	1566.4	115.6
Tagdate×Weight	1	1568.0	117.3
Tagdate	1	1568.9	118.1

***Escapement / Conversion*.** – The escapement / conversion results for the 2007 studies can be used for several evaluations. First, the results can be compared among tag types. This requires similar start and end points of each passage segment or reach. Because dam tailraces and fishway entrances can not be efficiently monitored with PIT systems, comparisons between tag types are necessarily limited to release and top-of-ladder sites. Table 15 shows release to top-of-ladder metrics for the 1997-2002 and 2007 telemetry studies and the 2005-2007 HDX-PIT studies. Second, it is important to compare lamprey conversion estimates at Bonneville Dam upstream from the tailrace. Evaluations of fishway modifications, including development of lamprey passage structures (LPS), are most instructive if events that occur in the tailrace can be excluded (i.e., the effects of predation and migration downstream from Bonneville Dam). Table 16 presents conversion estimates – synonymously termed 'passage efficiency' in previous years – for the telemetry studies, from lamprey approach at Bonneville Dam fishway antennas to top-of-ladder antennas. No comparable metric was possible with the HDX-PIT data.

Table 15. Summary of reach conversion estimates for radio-tagged and HDX-PIT tagged lamprey released downstream from Bonneville Dam and recorded at or known to pass top-of-ladder sites at lower Columbia River dams. 1997-2002 data are from telemetry study annual reports (e.g., Ocker et al. 2001) and 2005-2006 HDX-PIT data are from Daigle et al. (2008).

	Conversion estimates Radiotelemetry						
	1997	1998	1999	2000	2001	2002	2007
Release	147	205	199	299	298	201	398
Top BO	0.33 (49)	0.36 (73)	0.41 (82)	0.41 (123)	0.43 (129)	0.46 (92)	0.21 (83)
Top TD	0.11 (16)	0.12 (24)	0.13 (25)	0.23 (70)	0.23 (68)	0.23 (46)	0.05 (21)
Top JD	0.02 (3)	0.01 (3)	0.02 (3)	0.08 (23)	0.09 (27)	0.08 (17)	0.02 (9)
		HDX-PIT					
	2005	2006	2007				
Release	841	2000	757				
Top BO	0.53 (446)	0.41 (822)	0.52 (393)				
Top TD	-	0.28 (558)	0.33 (246)				
Top JD	-	0.19 (382)	0.17 (129)				
Top MN	0.05 (40)	0.04 (80)	0.05 (35)				

Table 16. Number of radio-tagged lamprey released below Bonneville Dam from 1997-2002 and in 2007, mean lamprey length and weight, number of lamprey detected approaching fishway antennas at Bonneville Dam, percentage of tagged fish recorded passing the dam (conversion rate or passage efficiency), and the median travel time (days) to pass the dam. Pre-2007 data from Moser et al. (2002, 2003, 2004 and 2005). The navigation lock was unmonitored in 2007.

	Year						
	1997	1998	1999	2000	2001	2002	2007
# Released	147	205	199	299	298	201	398
Mean Length (cm)	70	70	71	70	77	72	66
Range	60-80	59-79	65-78	62-80	62-82	60-80	53-86
Mean Weight (g)	-	545	571	570	588	612	466
Range	> 450	420-830	475-755	405-825	380-880	440-790	256-810
Detected at Bonneville	88%	89%	92%	87%	93%	96%	68%
Conversion rate[1]	38%	40%	45%	47%	46%	48%	31%
Median Dam Passage	4.9 d	5.7 d	5.5 d	4.4 d	11.0 d	9.0 d	3.0 d

[1]'passage efficiency' in previous years

Using the conversion estimate from release to top-of-ladder sites at Bonneville Dam, the 2007 telemetry estimate of 21% was considerably lower than in previous telemetry studies (33-46%) and was lower than the HDX-PIT estimates from 2005-2007 (41-53%) (Table 15). Multi-dam conversion estimates across all lamprey passage studies in the lower Columbia River also suggest that the 2007 conversion estimates for radio-tagged fish were broadly lower. In part, this reflects smaller mean lamprey size in the 2007 telemetry sample and the pattern of lower passage success for smaller radio-tagged fish. The mean fork length for radio-tagged lampreys in 2007 (66 cm) was 4-11 cm (6-17%) smaller than in the 1997-2002 samples. Similarly, the mean weight in 2007 (466 g) was 79-146 g (17-31%) smaller than means in previous telemetry samples. As described above, the 2007 telemetry results may also have been compromised by transmitter failure or detection problems.

Individual dam conversion estimates for HDX-PIT tagged fish in 2005 and 2006 were 41-53% from release below Bonneville Dam to pass the dam, and 62-76% from detection in a McNary Dam fishway to the top of McNary Dam (Daigle et al. 2008). The 2007 HDX-PIT results were very similar to these earlier HDX-PIT study results, with conversions of 52% at Bonneville Dam and 67% at McNary Dam. HDX-PIT tagged lampreys in 2007 were smaller (on average) than those HDX-PIT tagged in 2005-2006, but differences were not as great as for the radio-tagged fish. Study lampreys in 2007 were 3-5% shorter (65 cm vs. 67-68 cm) and 8-12% lighter (445 g vs. 482-500 g) than in the previous two years. Despite the size differences, conversion estimates from the release site past upstream dams in 2007 were similar to or higher than in 2005 and 2006 (Table 15). In 2007, estimates between top-of-ladder sites at pairs of dams were 63% (Bonneville-The Dalles), 52% (The Dalles-John Day), and 27% (John Day-McNary). In contrast to the multi-dam reaches, these estimates were lower than the 2006 HDX-PIT estimates of 68%, 68%, and 34%, respectively (Daigle et al. 2008) and may reflect some effect of the smaller fish in the 2007 sample. As of this writing, data were unavailable for any lamprey that overwintered in the lower Columbia River as these fish typically do not resume upstream migration until later in the year. Based on the 2005-2006 HDX-PIT results, we expect conversion estimates described here will increase by a few percentage points when the data are finalized.

Comparisons across radiotelemetry study years also indicate that the 2007 conversion estimate from release to approach Bonneville Dam fishways (i.e., through the tailrace) was considerably lower (68%) than in earlier telemetry studies (87-96%) (Table 16). It is not clear whether this was also primarily size related, or if other factors (i.e., increased pinniped predation, Tackley et al. [2008]) were important. The conversion estimate from fishway approach to exit from the top of a fishway was also lower in 2007 (31%) than in previous telemetry studies (38-47%), though this difference was not as large. Detailed analyses of lamprey movements through entrance areas, collection channels, transition pools, and up ladders and past count stations suggest that the radio-tagged lamprey in 2007 performed similarly to or at lower efficiencies than in previous years in most fishway segments (Johnson et al. *in review*).

Both the telemetry and HDX-PIT conversion data in 2007 consistently indicated higher passage success for larger fish. This pattern held across study reaches and did not appear to be related to migration timing as there were minimal size×timing correlations. This finding was consistent with the HDX-PIT results described in Daigle et al. (2008). In 2007, the relationship between fish size and upstream conversion was not statistically significant in all reaches, but this was due (at least in part) to sample size limitations. Several hypotheses may explain the greater success of larger fish. First, larger fish may be stronger swimmers more able to ascend through the difficult passage environments at dams (e.g., Mesa et al. 2003). Second, larger fish may have greater energetic reserves, allowing for longer upstream passage distances before they seek spawning areas or initiate overwintering behavior. Third, larger fish may be disproportionately from upriver populations, though this would be at odds with a general consensus that anadromous lampreys (Pacific and other species) are panmictic (Bryan et al. 2005; Almada et al. 2008; Goodman et al. 2008), lacking strong genetic or geographic stock structure. However, preliminary results from new genetic tests indicate some stock structuring in Columbia basin Pacific lamprey (Lin et al. 2008), suggesting additional genetic testing of Columbia-Snake River lamprey may be necessary to resolve the stock question.

Importantly, these hypotheses are not mutually exclusive. It is possible, for example, that higher passage success by larger fish was related to both swimming ability (or energetic status) and some underlying stock structure. Regardless of the mechanism, efforts to increase lamprey passage success at dams should consider operations or structures that can accommodate smaller individuals. As an example, the high velocity areas near adult fishway entrances have been an area of difficult lamprey passage (Moser et al. 2002b), and such velocity barriers may be especially difficult for smaller fish. An experimental flow reduction from Bonneville fishway entrances at night significantly improved lamprey entrance efficiency, presumably by allowing weaker swimmers to enter more easily

(Johnson et al. *in review*). Similarly, lamprey passage structures installed in the Bradford Island ladder at Bonneville Dam allow lamprey to circumvent high velocity areas in the serpentine weir sections of the ladder. In these examples, both operational (fishway entrance velocity) and structural (bypass systems) changes potentially increase overall dam conversion for adult lamprey.

We found little evidence for broad-scale environmental control over dam or multi-reach conversion rates. Daily conversion estimates and estimates based on 10-d release blocks were widely variable, and neither river discharge nor temperature was associated with conversion success in more than one study reach. In the two statistically significant results, HDX-PIT fish that successfully passed from Bonneville Dam past The Dalles Dam encountered slightly warmer temperatures than fish that did not pass The Dalles and successful fish in the John Day-McNary reach encountered slightly higher flow than unsuccessful fish. The lack of pattern at a broad scale does not imply that fine-scale environmental conditions were unimportant. Proximate effects such as water velocity and volume near fishway entrances or near spillways likely impact lamprey energetics and behaviors, with consequent effects on conversion rates. Broad metrics like total river flow may poorly represent the specific conditions encountered by individual fish. We also emphasize that the strong correlations among flow, water temperature and date of migration make it difficult to isolate cause and effect at these scales.

Dam-to-dam and longer reach conversion estimates are valuable for making generalizations about lamprey passage success and identifying potential problem areas. However, a more informative interpretation of conversion estimates will require a better understanding of the distribution and size of Pacific lamprey spawning populations in the Columbia basin. Pacific lamprey historically coincided spatially with anadromous salmonids in the basin (Close et al. 1995), but there has been little systematic study of current populations (see Cochnauer and Claire 2002; Moser and Close 2003; Graham and Brun 2005). The PIT tag data from 2005-2007 suggests that relatively large proportions of the runs may enter tributaries between John Day and McNary dams (i.e., the John Day and Umatilla rivers). The relatively high conversions between Bonneville-The Dalles and The Dalles-John Day dams (~68%) suggest that more modest numbers of fish likely entered the Deschutes River and possibly tributaries to the Bonneville reservoir. Telemetry results in the Moser et al. studies indicated that ~25-30% of lamprey that passed The Dalles Dam entered the Deschutes River, but there was little apparent use of Bonneville reservoir tributaries in those studies. A more complete accounting of fish fates, including better discrimination between mortality, harvest and tributary turn-off will be needed to fully interpret conversion estimates (e.g., Keefer et al. 2005).

Passage Rates. – HDX-PIT tagged lamprey took a median of 31 days to pass from release near Hamilton Island to the top of McNary Dam in 2007 which is in the middle of the range of estimates from similar studies in 2005-2006 (Daigle et al. 2008). These times were 3-5 times longer than those recorded for radio-tagged summer Chinook salmon (*O. tshawytscha*) and sockeye salmon (*O. nerka*) migrating during the same season (summer) over approximately the same distance in previous years of telemetry studies (Keefer et al. 2004; Naughton et al. 2005).

Lamprey passage times at dams are typically much longer than those recorded for salmonids. In the several lamprey telemetry studies (including 2007), median passage times at dams were 4-8 d at Bonneville, 2-4 d at The Dalles and ~ 2 d at McNary dams (Moser et al. 2002b; Cummings 2007). Times in the earlier studies were generally calculated from the first detection at a receiver in a fishway, thus excluding time fish initially spent in tailrace areas searching for passage routes.

The 2007 radio-tagged lamprey passed relatively quickly through reservoirs, as has been reported in previous studies. Median times in 2007 were < 4 d through the Bonneville reservoir and < 2 d through The Dalles reservoir. These times are approximately half as long as those recorded for summer Chinook salmon (Keefer et al. 2004), suggesting both lamprey and salmonids move relatively rapidly through reservoirs but are significantly slowed while passing dams.

Median HDX-PIT tagged lamprey passage rates through reaches with a single dam and reservoir ranged from 10-18 $km \bullet d^{-1}$ and were 12-14 $km \bullet d^{-1}$ through multi-dam reaches. Maximum rates past multiple dams were > 35 $km \bullet d^{-1}$. Overall, these rates were higher than median (11 $km \bullet d^{-1}$) and maximum (21 $km \bullet d^{-1}$) passage rates recorded for radio-tagged lamprey in the unimpounded John Day River (Robinson and Bayer 2005) and were consistent with those for radio-tagged Columbia River fish in 2007 and in previous years (e.g., Moser and Close 2003). The fastest migrating lamprey passed at about the same rate as an average summer Chinook or sockeye salmon (Keefer et al. 2004; Naughton et al. 2005).

We did not find strong correlations between migration rates and lamprey size, either through single dam-to-dam reaches or over longer reaches. However, there was evidence for increased passage rates later in the migration seasons and slower passage when Columbia River flow was high. Because flow decreased through the migrations in both years, separating migration timing and environmental effects was difficult. Robinson and Bayer (2005) found similar seasonal patterns of faster migration late in the season for lampreys in the John Day River. Similarly, Moser et al. (2004) Daigle et al. (2008), and Keefer et al. (*in press*) found lamprey passage rates at dams were positively (if weakly) correlated with both temperature and time of year.

Overall, environmental conditions and lamprey size explained only small proportions of the lamprey passage time variability in 2007. This is consistent with previous lamprey summaries and suggests that other more fundamental factors are important. The underlying challenges associated with dam passage for lamprey — independent of river environment or migration timing — may be the primary drivers behind the considerable passage time variability we recorded. These potential factors include nocturnal behaviors, among-population differences, individual physiology, or maturation status. Quantifying tributary entrances and final fates of lamprey would also improve our understanding of their migration behaviors and dam-to-dam conversion rates.

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Appendix A. Maps of monitoring sites in 2007.

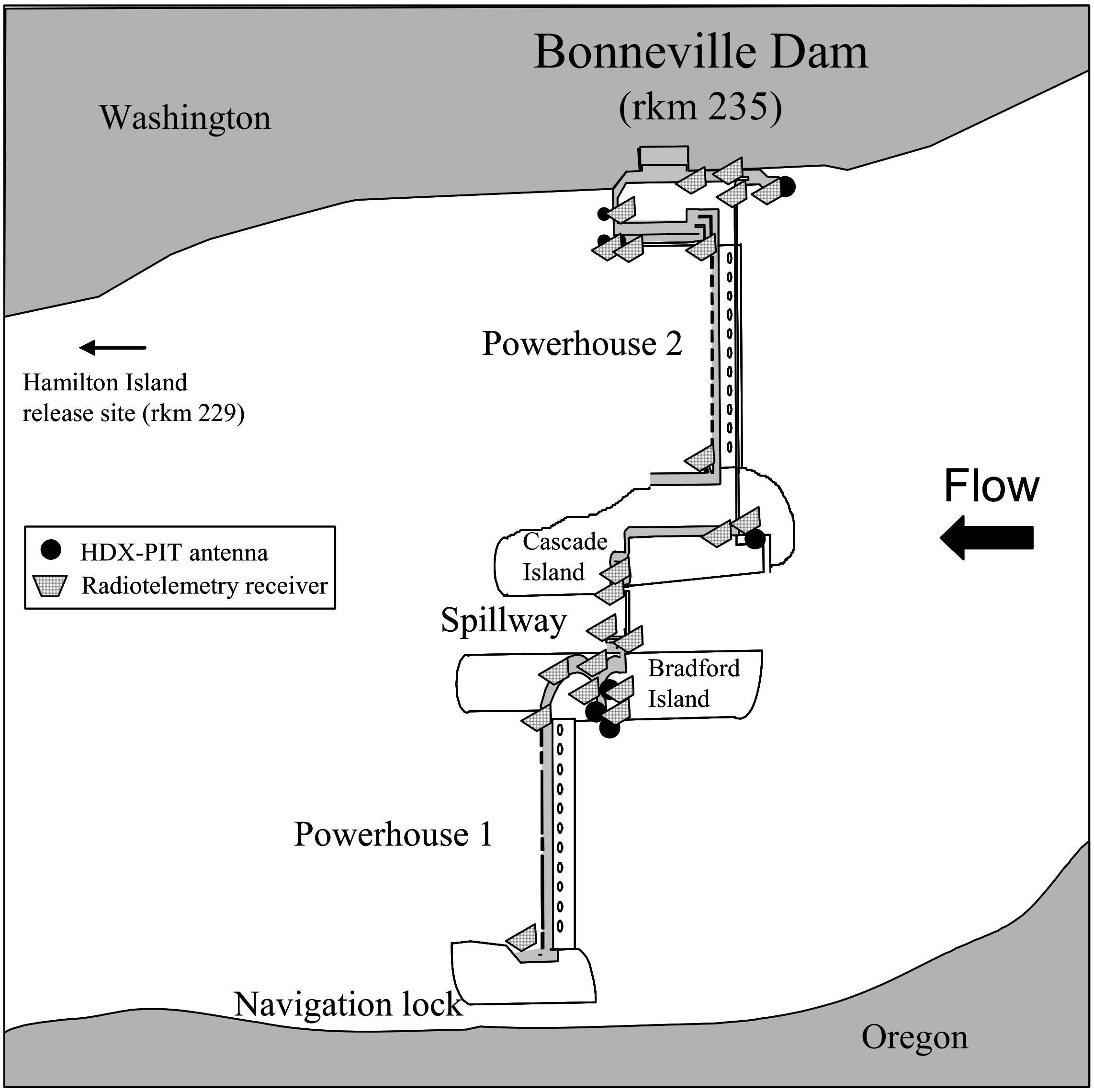


Figure 1. Study area at Bonnevillle Dam on the Columbia River in 2007. Black circles represent HDX-PIT monitoring sites and hashed symbols represent underwater radiotelemetry receiver sites. Telemetry sites supported multiple antennas.

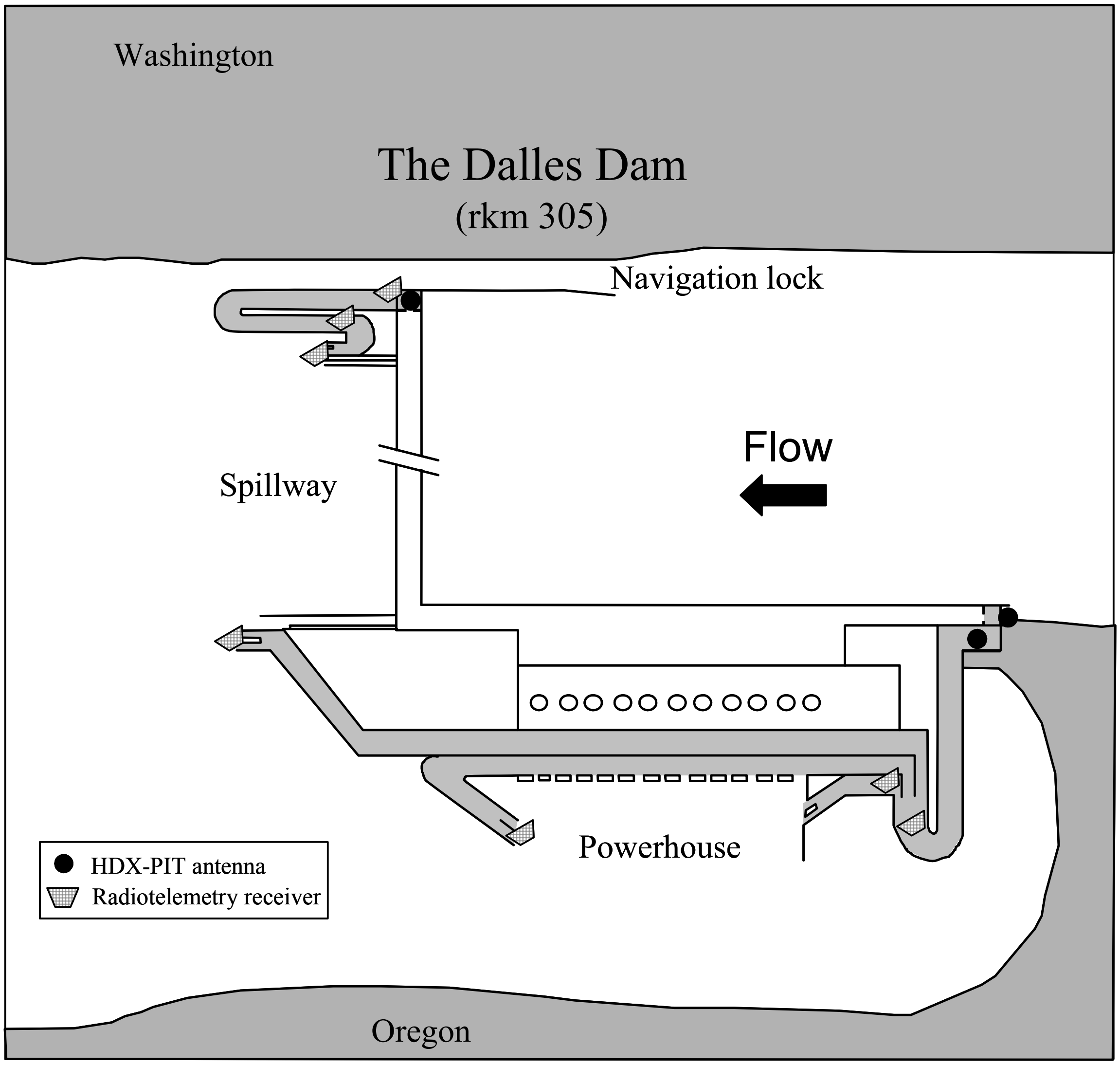


Figure 2. Study area at The Dalles Dam on the Columbia River in 2007. Black circles represent HDX-PIT monitoring sites and hashed symbols represent underwater radiotelemetry receiver sites. Telemetry sites supported multiple antennas.

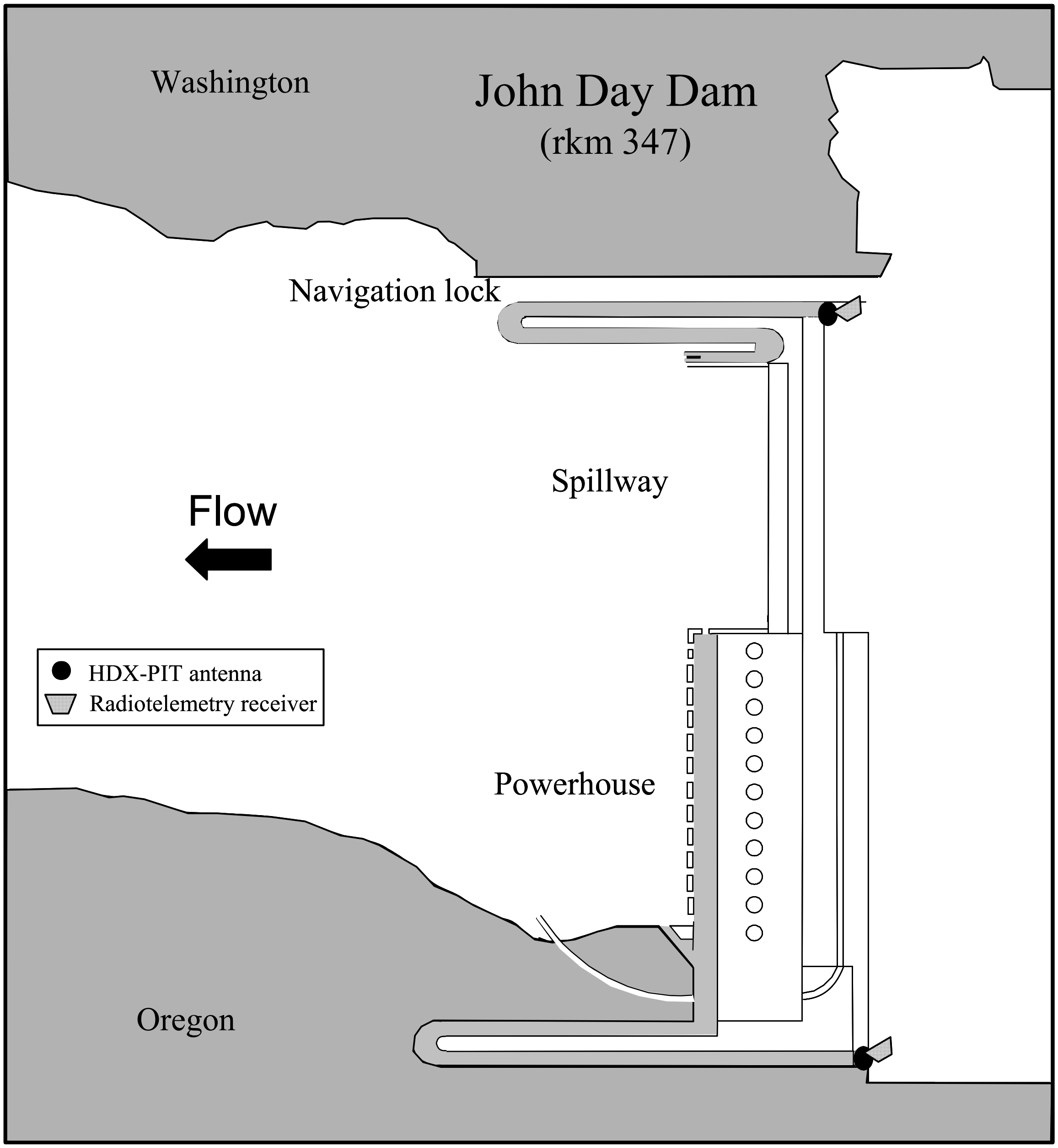


Figure 3. Study area at John Day Dam on the Columbia River in 2007. Black circles represent HDX-PIT monitoring sites and hashed symbols represent underwater radiotelemetry receiver sites. Telemetry sites supported multiple antennas.

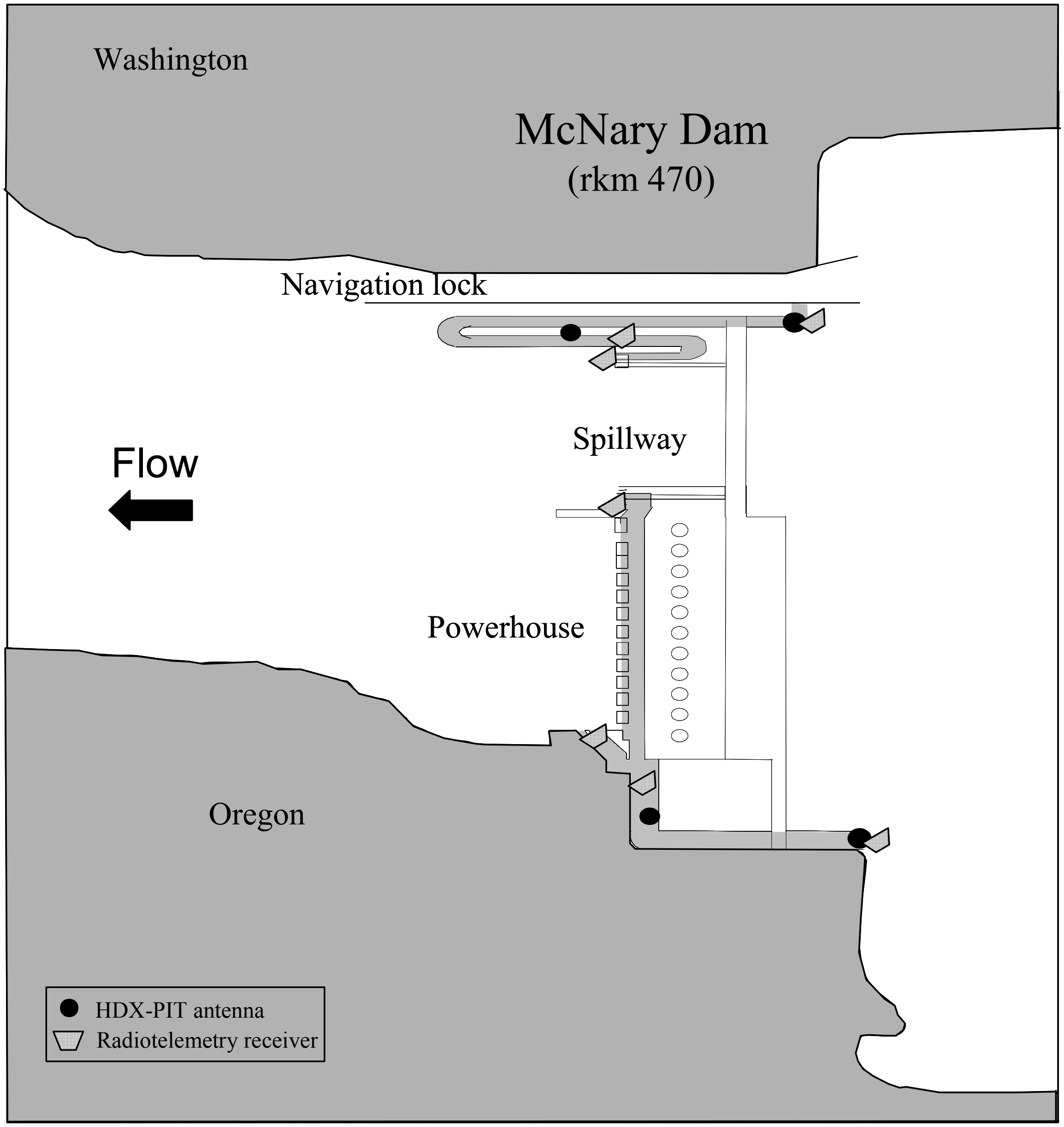


Figure 4. Study area at McNary Dam on the Columbia River in 2007. Black circles represent HDX-PIT monitoring sites and hashed symbols represent underwater radiotelemetry receiver sites. Telemetry sites supported multiple antennas.

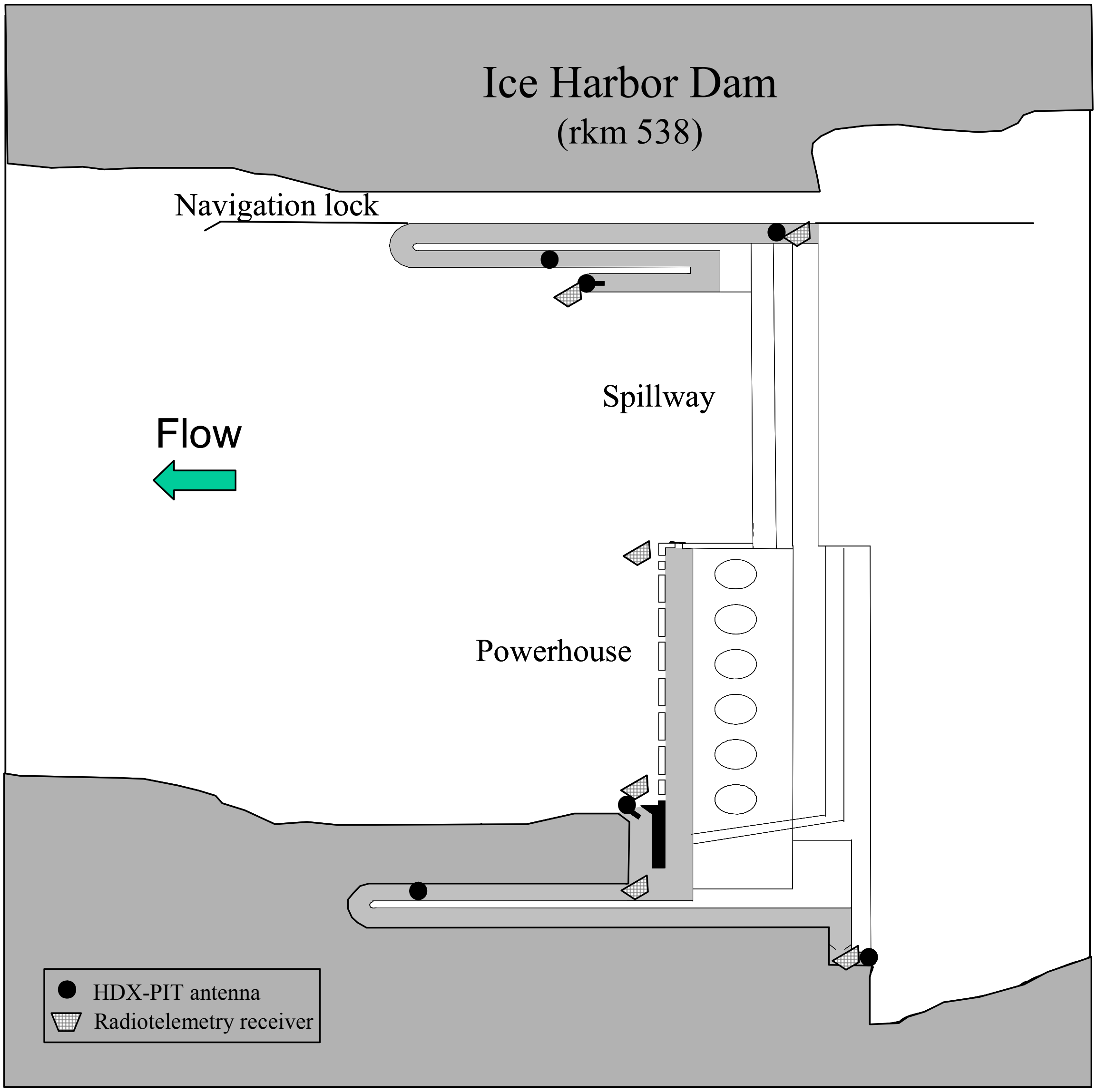
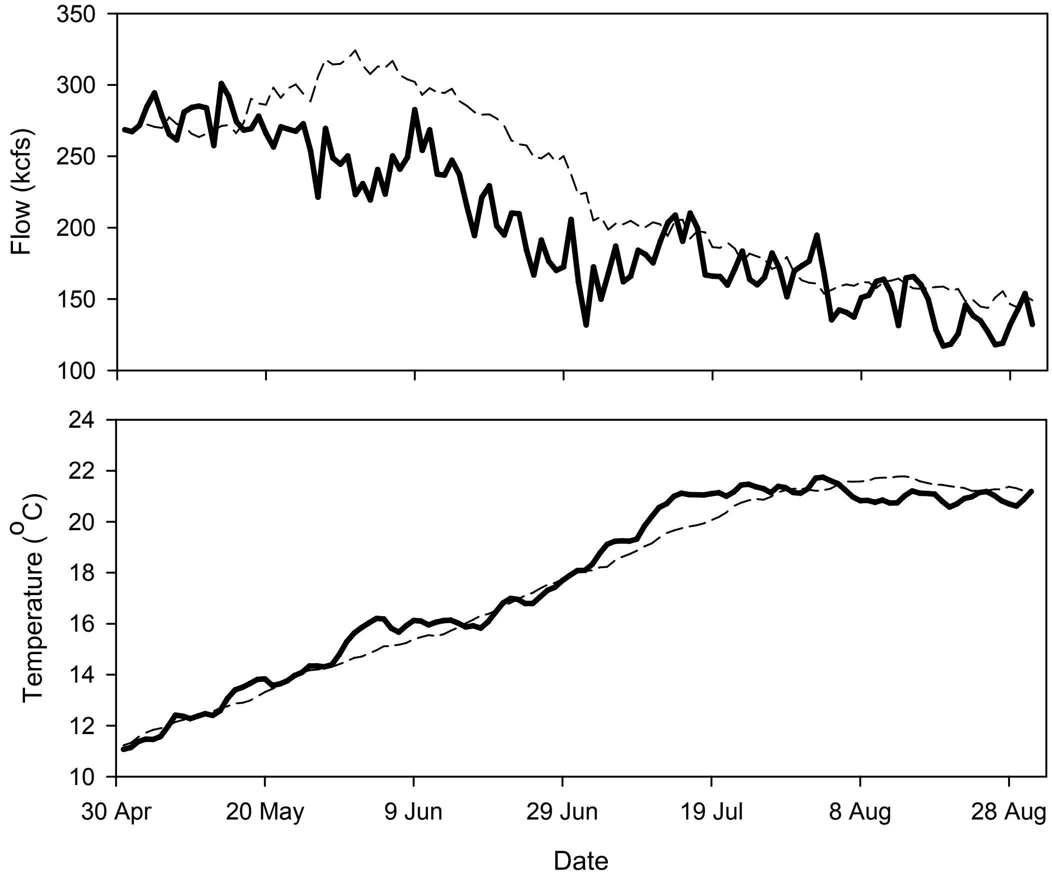


Figure 5. Study area at Ice Harbor Dam on the Snake River in 2007. Black circles represent HDX-PIT monitoring sites and hashed symbols represent underwater radiotelemetry receiver sites. Telemetry sites supported multiple antennas.

Appendix B. 2007 Columbia River flow and temperature profiles.



Appendix Figure 1. Mean daily Columbia River flow (kcfs) and temperature (°C) at Bonneville Dam in 2007 (solid line) and for the 1997-2006 average (dashed line).